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Community assembly and the sustainability of habitat offsetting targets in the first compensation lake in the oil sands region in Alberta, Canada

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ABSTRACT

Resource development can have a negative impact on species productivity and diversity through the loss and fragmentation of habitat. In many countries, developers are required by law to offset such impacts by replacing lost habitat or providing other forms of compensation. In the case of broad scale development, offsets often cannot be constructed to replace lost habitat “like-for-like” (i.e., they are not ecologically equivalent). In freshwater ecosystems, one approach to habitat offsetting is to create new lake ecosystems, called compensation lakes, to replace lost riverine habitat. In this study, we use a long-term data set (2008–2015) of fish and benthic invertebrate communities from Canada's first compensation lake in the oil sands region of Alberta, to address (1) whether the assembly of the fish community has a trajectory that is influenced by management activities and (2) determine whether the community composition in the habitat offset is common in natural lake ecosystems within the region. We find a significant decline in the mean trophic level of the lake, where 61.9% of the variation in trophic level is explained by time indicating a strong structuring influence on fish communities. This outcome has enabled the compensation lake to meet overall and single species productivity targets, but we find that the species assemblage and composition is not common within the region. A combination of the founding species community and reduced connectivity of the lake has contributed to the current fish community structure, which may be problematic for the sustainability of the habitat offsetting targets. Our study highlights the need to establish multiple conservation guidelines, using both productivity and diversity based metrics, to provide the best ecological equivalency, which can produce better function, resilience and health within focal species communities in habitat offsets that are not “like-for-like.”

1. Introduction

Globally, one of the major drivers of declines in the productivity and biodiversity of species, and their habitats, is through land-use change (Dirzo et al., 2014; Sala et al., 2000). One form of land-use change that can cause such habitat loss is resource development (Bull et al., 2013; Minns, 2015). When the avoidance, minimization, and mitigation of this impact is not possible, habitat offsets may provide a solution to achieve no net loss of a particular targeted habitat feature (BBOP, 2012; IFC, 2012). Many countries have adopted habitat offsetting policies (e.g., Canada, United States, Europe, Australia, New Zealand, and United Kingdom), where the ideal goal is ecological equivalency, such that offsets are done in a manner which replaces habitats “like-for-like” in areas in close proximity to where those habitats were displaced (Bull et al., 2015; Bull et al., 2013). When ecological equivalency cannot be achieved with habitat offsets, such as when the extent, duration and intensity of the impacts are sufficiently broad in spatio-temporal scale (e.g., surface mining, urban development), new offsetting currencies and flexibility may be needed (Bull et al., 2015; Habib et al., 2013).

Underpinning the management goal to maintain productivity and biodiversity in habitat offsetting practices are the many ecological processes supported by species assemblages and community structure, which will provide desirable levels of resilience, function and health in ecosystems (Bull et al., 2015; Bull et al., 2013; DeFries and Nagendra, 2017). Of note, higher species diversity can generate increased functional diversity (Tilman et al., 1997), which in turn provides communities with a set of species that have differential responses to environmental variability (McCann, 2000). Thus, one might expect that comparable ecosystem resilience and function would result from maintaining biodiversity in habitat offsets (Dudgeon et al., 2006; Folke et al., 2004; Vander Zanden et al., 2006). Moreover, the goal of habitat offsets is to emulate natural ecosystem processes, which will require comparable species diversity to what is lost to development (Bull et al., 2013). A major difficulty in achieving this outcome is that successional

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or community assembly processes in many new ecosystems is not well resolved with many taxa (Palmer et al., 1997). In order to reduce this uncertainty, single species management approaches may be preferred (where interactions may be better resolved and there is greater certainty); however, there is the danger that this may contribute to lower functional diversity, which could increase variability in the ecosystem (e.g., fisheries productivity), preventing the establishment of a resilient and functioning ecosystem (DeFries and Nagendra, 2017; Lambeck, 1997).

In Canada, companies are required by law to develop offsetting strategies to compensate for fish habitat loss in aquatic ecosystems (Minns, 2006, 2015; Rice et al., 2015). Specifically, the current policy states that the creation of habitat offsets is required when unavoidable serious harm to fish or losses in Commercial, Recreational and Aboriginal (CRA) fisheries productivity occurs (Rice et al., 2015). Thus, the offsetting currency is CRA fisheries productivity (which can be simply defined as $kg{\cdot}yr^{-1}$) that is supported by compensating for fish habitat loss. Moreover, the CRA fisheries productivity is defined as losses to a specific fishery and the fish species that support that fishery, which broadly includes all fish species within the ecosystem (DFO, 2013, 2014). To offset the loss of fish habitat that is originally in lotic and lentic freshwater ecosystems the construction of new lake ecosystems, hereafter referred to as compensation lakes, is gaining interest. In the oil sands region in northern Alberta, which represents the third largest oil reserves in the world, industrial activities have been increasing dramatically within the past couple decades, which has led to an increased footprint, or impact, on aquatic ecosystems (Schwalb et al., 2015; Webster et al., 2015). In response, there has been a subsequent initiation of many compensation lake projects within the region (five constructed lakes and five or more are currently within the planning process; Court Berryman, Department of Fisheries and Oceans, Edmonton, Alberta, *personal communication*, 2016), making it one of the most active areas in Canada within the scope of habitat offsetting via compensation lakes (see Fig. 1A). Fish communities in the oil sands region, which is in the lower Athabasca watershed, are not speciose or highly productive ecosystems (Nelson and Paetz, 1992). However, despite the apparent simplicity in terms of fish diversity, there is still much uncertainty related to processes that can alter the establishment and trajectory of the resulting fish community and ecosystem (DeFries and Nagendra, 2017; Matthews and Marsh-Matthews, 2016).

Much uncertainty remains within the management framework of offsetting practices, including: the assembly and stocking of fish communities, the long-term sustainability of management targets, identifying the importance of the role and sequence of structuring processes, establishing an appropriate baseline or reference system, among many others aspects (Minns, 2015; Vander Zanden et al., 2006). Specifically, the assembly of fish communities may include stochastic (e.g., priority effects, drift) and deterministic (e.g., competition, predator-prey relationships, connectivity) processes that can shape the resulting state of a community and ultimately the ecosystem (Carpenter et al., 2001; Matthews and Marsh-Matthews, 2016; Milner et al., 2011; Vander Zanden et al., 2006; Webster et al., 2015). For instance, the order of introduction (i.e., priority effects) and subsequent species interactions can play a major role in determining the outcome of fish communities and the resulting long-term productivity and/or diversity within the system (Matthews and Marsh-Matthews, 2006; Vander Zanden et al., 2006). Moreover, the benefits of balancing top-down and bottom-up control within the ecosystem cannot be overstated, where the establishment of predator-prey interactions early on in the assembly process can provide more stability and resilience in the composition of fish communities (Brashares et al., 2010; Carpenter et al., 2001; Estes et al., 2011). One way to assess the influence management has on community assembly is by using whole-ecosystem experiments to provide insight, where conservation management decisions can have impacts on ecosystem outcomes.

In this study, we investigate the initial assembly of the fish and benthic invertebrate communities using a long-term data set (2008–2015) from the first compensation lake established within the oil sands region of northern Alberta. Specifically, we address: (1) whether the assembly of the fish community has a trajectory that is influenced by management activities and (2) determine whether the community composition in the habitat offset is common in natural lake ecosystems within the region. Addressing these questions will help to outline the potential processes that govern fisheries productivity in compensation lake ecosystems during the first years following establishment. Moreover, we provide context on the contribution of management decisions during community assembly and assess whether productivity focused management objectives maximize ecological equivalency to achieve long-term sustainability of the fishery and ecosystem.

2. Methods

2.1. Study area

Horizon Lake is a compensation lake, which was established along the Tar River within the lower Athabasca watershed in 2008 (Fig. 1). The compensation lake was created to offset the loss of lotic fish habitat that previously existed prior to mining operations (see light grey polygon in Fig. 1). Horizon Lake has a surface area of approximately 77 ha, with an average depth of 7.2 m and a maximum depth of about 23 m (Jiang et al., 2015). The design of the compensation lake included the establishment of deep channels, shoals, and multiple substrates including sand, cobble and gravel to promote habitat heterogeneity and fisheries productivity. While the initial design was based on promoting overall fisheries productivity (i.e., multiple species), there is also a desire to promote Arctic Grayling (*Thymallus arcticus*) productivity. Thus, the colonization of several species (namely higher trophic level species) has not been facilitated in order to assess potential Arctic Grayling productivity within the compensation lake. The potential shift in focus reflects a need to promote Arctic Grayling productivity within Alberta, as they are experiencing population declines and range recession within the province (ASRD, 2005). Horizon Lake has a major inflow (Upper Tar River) and outflow (Lower Tar River), where fish may freely move upstream, however, they are prevented from moving downstream due to the presence of a screen on a submerged outlet. The long-term management plan (30+ years) is to reconnect Horizon Lake to the Athabasca watershed. Water residence time in Horizon Lake can be a few weeks to months depending on whether it is wet or dry season and the lake is covered by ice from mid-November to early May. The hydrodynamics of Horizon Lake have been studied in detail by Jiang et al. (2015).

2.2. Fish and benthic invertebrate sampling

Fish and benthic invertebrate communities in Horizon Lake have largely colonized from the Upper Tar River, with the exception of 4749 Fathead minnows (*Pimephales promelas*) and 1630 Brook sticklebacks (*Culaea inconstans*) that were released into Horizon Lake from a nearby lake (Calumet Lake) in 2009 (Fig. 1). We used historical data records spanning 2008–2015, where sampling for fish and benthic invertebrates commenced immediately after the establishment of Horizon Lake in the fall of 2008 and occurred semi-regularly depending on the location and type of sampling (e.g., fish vs. invertebrates; Table S1). The most consistent sampling occurred annually during the fall season (Table S1). Fish were collected using standardized Fall Walleye Index Netting (FWIN), which consists of a gill net of 8 panels of differing mesh sizes (1, 1.5, 2, 2.5, 3, 4, 5, and 6 in.), where each panel is 1.8 m wide and 7.6 m long, making the full length of the net 60.8 m. FWIN netting is the standard sampling protocol used by the province of Alberta (AEP, 2015) as well as elsewhere (Morgan, 2002) to determine fish community composition. Sampling was conducted in at least 3 or 4 locations (some times more) in 1–3 seasons per year and repeated for several days at a

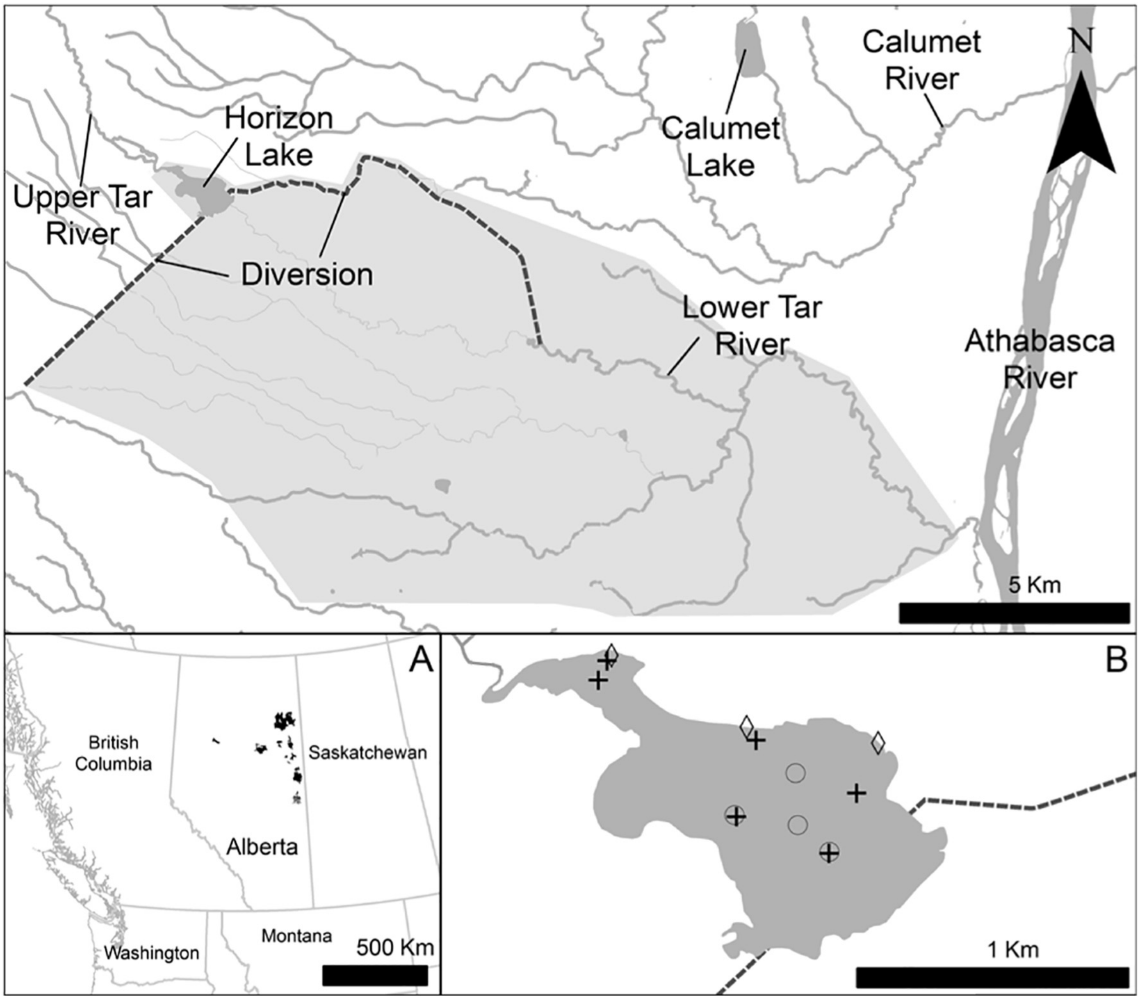

Fig. 1. An overview of the study area showing the location of the compensation lake (Horizon Lake; 111°57′49.44″W, 57°23′10.82″N). Light grey lines delineate rivers and creeks that show limited or no flow due to development. The light grey polygon designates the Harmful Alteration, Disruption or Destruction (HADD) of fish habitat boundary. Gill net sample sites are denoted by open circles, benthic invertebrate sample sites by the crosses for Ekman grab and diamonds for kick net sample locations. The insets show all the (A) cleared, disturbed and reclaimed land that has been allocated for in situ, mines and upgraders in Alberta (AEMERA, 2007) and (B) a close up of sample locations in Horizon Lake.

time, with the net set at varying depths to target species in benthic and limnetic habitats (Fig. 1B and Table S1). Abundances of fish were standardized by the total soak time (days; abundance per day).

Benthic invertebrates were sampled in Horizon Lake every fall (Table S1) from open water using Ekman grab samples (area of 0.023 m^2) and littoral zones using kick net samples of kicking and collecting within an area of 1 m wide by 5 m in length. Sample locations were dispersed throughout the lake to sample varying depths using Ekman grabs (generally 5 grabs at 6 locations) and kick net samples (3 locations; Fig. 1B). Ekman grab samples were sieved using a 250 μm mesh box and kick nets had a mesh size of 500 μm. After collection, all samples were promptly preserved in 10% buffered formalin. The identification and abundance of benthic invertebrates were identified to levels recommended by Environment Canada (1998). Laboratory quality control was conducted on 10% of samples and results of this quality control show consistently > 98% sorting efficiency. Finally, as we are interested in comparing annual densities we standardized each technique as the number of individuals per square metre.

2.3. Data analysis

To determine how the fish community in the compensation lake changed through time we used Principal Components Analysis (PCA) to visualize fish community differences and similarities through time using the gill netting data for Horizon Lake. Prior to analysis, we removed species found in < 5% of samples (which included Slimy Sculpin (*Cottus cognatus*) and Finescale dace (*Chrosomus neogaeus*)) to remove the effect of rare species (Jackson and Harvey, 1989, 1993). We used PCA, as it is a form of unconstrained ordination that is suitable to short gradient analysis when community data is transformed (Legendre and Legendre, 2012). We also used a Hellinger transformation, which makes ecological data more amenable to Euclidean based methods such as PCA (Legendre and Gallagher, 2001). However, with one of our PCA models, which included seasonal species abundances from Horizon Lake, there was the presence of a horseshoe effect requiring a different transformation to be used, the log transform. Annual and seasonal differences in fish community composition were tested using a PERmutational Multivariate Analysis Of VAriance (PERMANOVA) with 999 permutations (Anderson, 2001). PERMANOVA is a Redundancy Analysis based significant test that uses a similar distance measure as PCA (here we use Euclidean distance), but constrains community data at sites by factors of interest (e.g., locations, time). Data can also be non-parametric as significance is determined through many permutations of the community data associated with the factors of interest to determine if associations with factors are more likely then compared to random (Anderson and Walsh, 2013).

A life history trait that can directly influence species interactions, ecosystem resilience, structuring processes, and ecosystem function is the trophic level of a species (Vander Zanden et al., 2006). Thus, we investigate fish community changes in Mean Trophic Level (MTL) in

Table 1
Summary of fish species found from 2008 to 2015 by their common name, code, scientific name, mean trophic level (standard deviation in brackets), and mean abundance for the compensation lake (gill netting (day^{-1})). The average seasonal range of abundance is provided in the brackets over the 8 years of samples.

Common name	Code	Species name	Mean trophic level[†]	Abundance
Arctic Grayling	ARGR	*Thymallus arcticus*	3.32 (0.40)	0.6 (0–3.2)
Brook Stickleback	BRST	*Culaea inconstans*	3.29 (0.47)	0.01 (0–0.1)
Fathead Minnow	FTMN	*Pimephales promelas*	3.13 (0.39)	0.02 (0–0.2)
Lake Chub	LKCH	*Couesius plumbeus*	3.38 (0.43)	1.7 (0–3.9)
Longnose Sucker	LNSC	*Catostomus catostomus*	3.11 (0.39)	15.4 (0–57.5)
Trout-Perch	TRPR	*Percopsis omiscomaycus*	3.38 (0.51)	0.3 (0–3)
White Sucker	WHSC	*Catostomus commersonii*	2.46 (0.16)	7.8 (0–44.6)

[†] Mean trophic level derived from FishBase randomized diet items resampling routine (Pauly and Sa-a, 2000).

Horizon Lake and used trophic levels of species from FishBase (see Table 1) and weighted the contribution of each species by their relative abundance from gill netting (or Catch-Per-Unit-Effort; CPUE) using the following relationship:

$$MTL_i = \frac{\sum_{ij} TL_{ij} CPUE_{ij}}{\sum CPUE_{ij}}$$

where Mean Trophic Level (*MTL*) is estimated for each season *i*, by multiplying the abundance (*CPUE*) for each species *j*, by their estimated Trophic Level (*TL*) and taking a weighted averaged (Pauly et al., 1998). To test for changes in MTL through time, we summarized the MTL for each seasonal sample from Horizon Lake ($n = 15$) using linear regression analysis. This was conducted using the *lm* function in the base functions for R software (Team, 2017).

We repeated the PCA technique with Hellinger transformation for the benthic invertebrate communities in open water and littoral habitats in Horizon Lake. Annual and sampling differences (Ekman grab and Kick net) for benthic invertebrate communities were also tested using PERMANOVA ($n = 999$ permutations). To test for concordance between annual mean values for fish and benthic invertebrate communities (both Ekman grab and Kick net samples separately) in Horizon Lake we use Procrustes analysis with PROcrustean randomization TEST (PROTEST; $n = 999$) (Peres-Neto and Jackson, 2001). Concordance is a *post-hoc* significance test, where the association between two PCA distance matrices can be tested for significance (through a permutations procedure (PROTEST)) that is able to test for associations in the temporal change between fish and benthic community data (Peres-Neto and Jackson, 2001). We adjusted all *p*-values across all tests for multiple comparisons using the Bonferroni method. This analysis is conducted using the *rda*, *adonis*, and *protest* functions in the *vegan* library in R software (Oksanen et al., 2016; Team, 2017).

Finally, we compared the species assemblage present within Horizon Lake to historical gill netting records available from 102 lakes in the lower Athabasca region (AEP, 2016) (Table S2). Gill netting records from 1967 to 2015 from these 102 lakes, were used to represent the natural variability of species assemblages within lakes in the lower Athabasca region, where a total 21 different species were found throughout all lakes (Table S2). We then used a subset of historical gillnetting records from 66 lakes, where fishing was conducted using FWIN and the duration of sets could be resolved, to compare to the mean community composition in Horizon Lake with other lakes found within the lower Athabasca watershed. We visualized similarities and differences using presence-absence of fish species to assess assemblage differences and Hellinger transformed abundances to compare differences in community composition using PCA. Prior to PCA analysis, we removed rare species (species found in < 5% of lakes; this included LogPerch (*Percina caprodes*), Spoonhead Sculpin (*Cottus ricei*), Finescale Dace (*Chrosomus neogaeus*), Northern Redbelly Dace (*Chrosomus eos*) and Cisco-Lake Whitefish hybrids (*Coregonus artedi* × *Coregonus clupeaformis*)) to remove the effect of rare species in our analysis (Jackson and Harvey, 1989). As a result only 16 species were used within the final analysis.

3. Results

Over the course of 8 years of monitoring only 7 species were observed in high abundance in Horizon Lake using gillnetting (Table 1 and Fig. S1). The PCA explained 92.0% of seasonal variation in fish community structure in Horizon Lake across the first two axes of variation (Fig. 2A). We found that the fish communities in Horizon Lake changed significantly on a year-to-year basis ($F_{1,14} = 8.865$, $p = 0.01$; Fig. 2A), however, there was no seasonal influence on the abundance and composition of fish species ($F_{2,14} = 0.884$, $p = 1.0$; Fig. 2A). Horizon Lake has a strong significant negative decline in the mean trophic level through time (Fig. 2B; adj-$R^2 = 0.619$, $p = 0.002$), which is due to increases in the abundance of lower trophic level species (Fig. S1). We observed a steady increase in the abundance and diversity of fish species in Horizon Lake (Fig. 3A and B). A peak in fish abundance was observed in 2013 (Fig. 3A) and fish diversity in Horizon Lake appears to plateau, starting in 2012, at 6 species (Fig. 3B).

Over the 8 years of this study we found 27 different benthic invertebrate taxon groups observed in > 5% of our samples (Table S2). From the establishment of Horizon Lake, we found that there is a steady increase in the density and diversity of benthic invertebrates within Horizon Lake (Fig. 3C and D). Further, we observe a large peak in abundance in 2012 and subsequent decline in abundance in 2013 (Fig. 3C). Our PCA explained 62.5% of variation in Benthic invertebrate community composition in both deep water (Ekman) and littoral (kick net) samples across the first two axes of variation and we found that the benthic community did not change significantly through time ($F_{1,15} = 2.679$, $p = 0.26$; Fig. 4). Both the deep water and littoral communities were initially dominated by *Chironomidae* and *Oligochaeta* (Table S2 and Fig. 4) and at about 2 years after the impoundment, Horizon Lake showed a marked increase in species diversity, when many (~10) other groups established in the lake (Table S2). Finally, deep water and littoral benthic invertebrate communities were significantly different ($F_{1,15} = 7.718$, $p = 0.01$; Fig. 4).

Fish and invertebrate communities showed similar abundance and diversity patterns relative to one another (Fig. 3). However, we found no significant concordance between the fish and benthic invertebrate communities in deeper regions of Horizon Lake ($m_{12} = 0.592$, $r = 0.639$, $p = 0.74$) and for our littoral kick net samples ($m_{12} = 0.521$, $r = 0.692$, $p = 0.27$). Finally, there was no significant concordance between benthic invertebrate communities from littoral and deep water habitats in Horizon Lake ($m_{12} = 0.343$, $r = 0.812$, $p = 0.09$).

The fish community found in Horizon Lake is not similar to most lakes within the lower Athabasca region in terms of species assemblage and composition (Fig. 5). In both instances Horizon Lake is beyond the 95% confidence ellipse in the biplots (Fig. 5). The first two axes of variation in the PCA explained 53.9% of variation in species assemblage across Horizon Lake and 102 lakes within the lower Athabasca region (Fig. 5A). The tendency was that most lakes within the region had at least some higher trophic level species, which may be considered top-predators, present within the species assemblage (Fig. 5A). However, Horizon Lake was one of only a few lakes characterized by having a community assemblage with Brook Stickleback (*Culaea inconstans*), Lake Chub (*Couesius plumbeus*), Fathead Minnows (*Pimephales promelas*), and Longnose Suckers (*Catostomus catostomus*). For community composition, the first two axes of variation in the PCA explained 42.5% in variation across 66 lakes in the lower Athabasca region (Fig. 5B). Horizon Lake was not similar to most lakes as it is characterized by having higher abundances of Brook Stickleback, Longnose sucker and

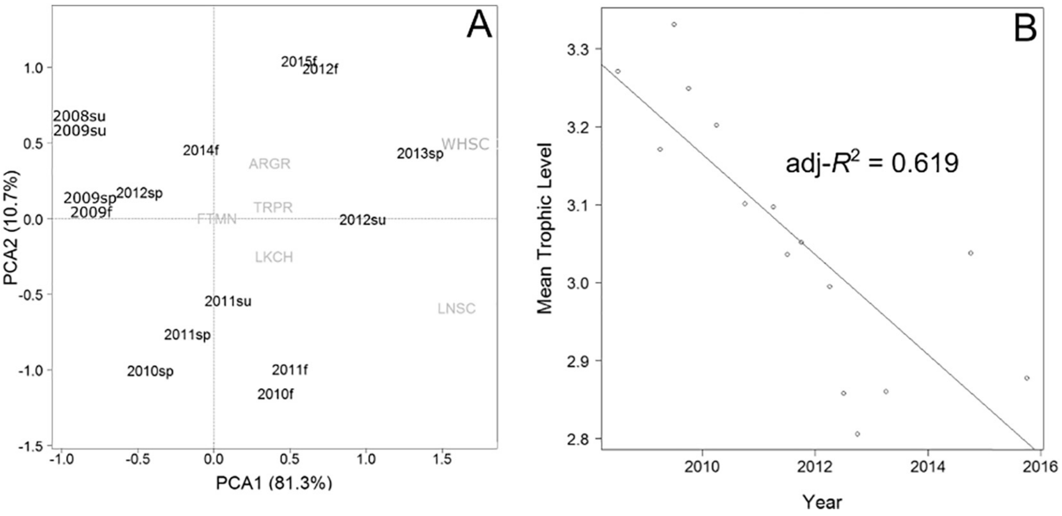

Fig. 2. (A) Principal component analysis using log transformed seasonal species abundances from gill netting samples in Horizon Lake labelled by year and season (sp – spring; su – summer; f – fall). Species codes can be found in Table 1. (B) Mean trophic level for seasonal fish samples from Horizon Lake (solid black line). The line represents a significant relationship ($p < 0.001$) between mean trophic level and time.

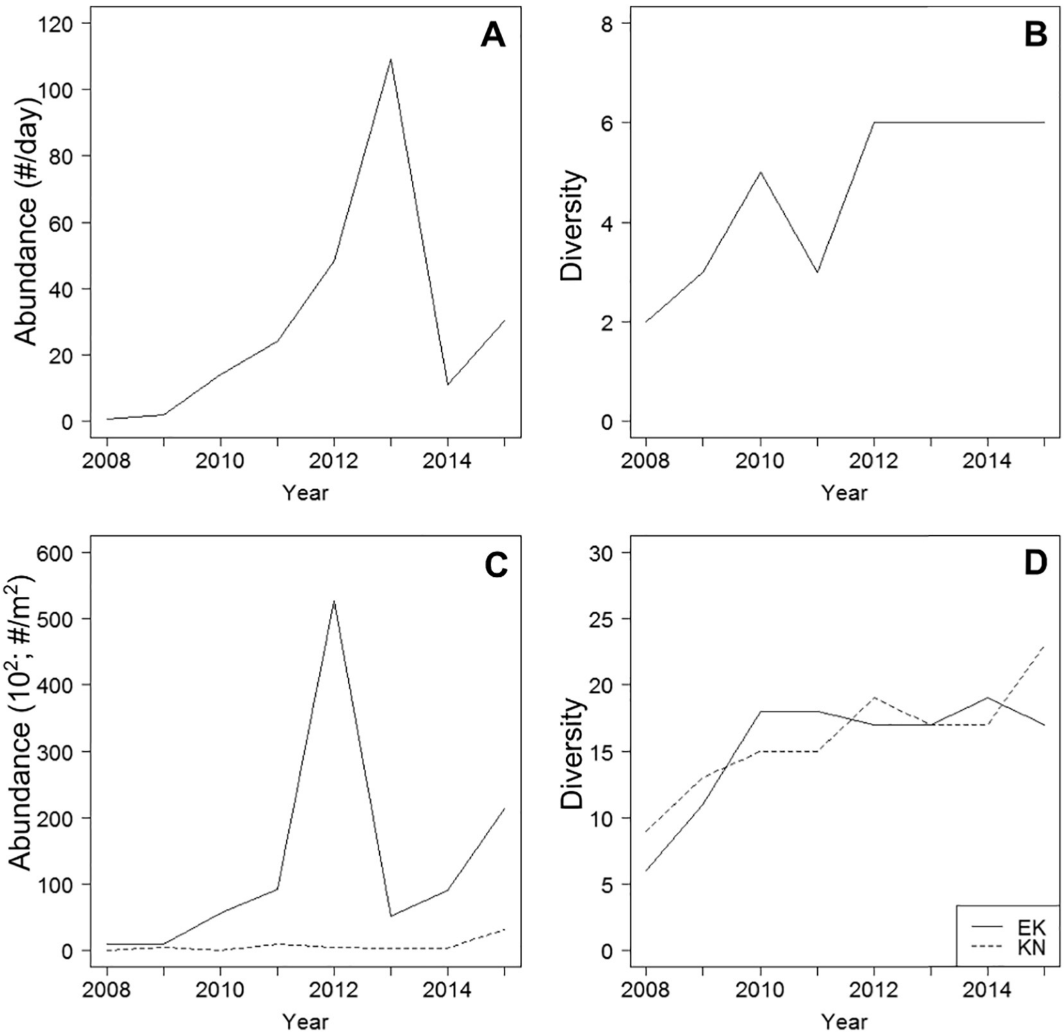

Fig. 3. The annual (A) mean density and (B) species diversity of fish species in Horizon Lake during the monitoring period of 2008–2015. Also shown is the corresponding annual (C) mean density and (D) diversity of benthic invertebrates during that period (EK-Ekman Grab; KN-Kick Net).

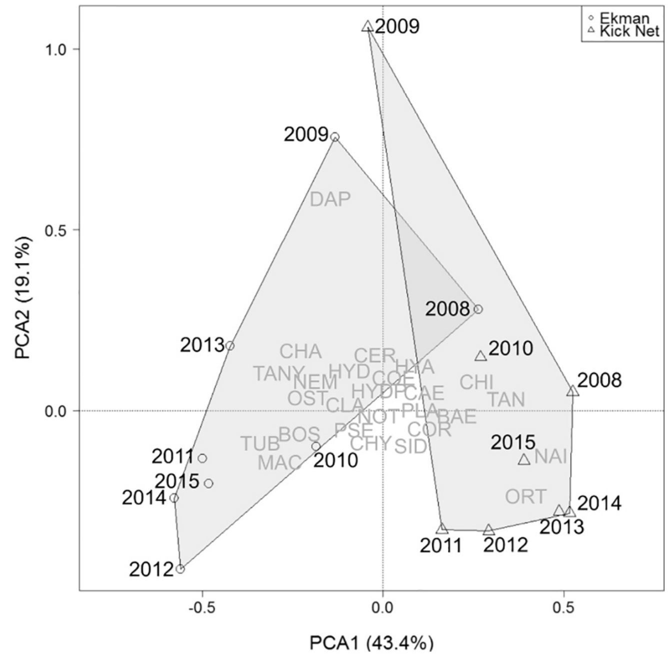

Fig. 4. Principal component analysis using Hellinger transformed distances of annual mean abundances of benthic invertebrates from both Ekman grab and Kick net samples in Horizon Lake. Grey polygons are the convex hulls (or the area in ordination space) where each sample method is represented. Sites are labelled by year and species codes can be found in Table S2.

White sucker (*Catostomus commersonii*) compared to other lakes in the region (Fig. 5B).

4. Discussion

The processes involved with the assembly of fish communities in newly created ecosystems and the degree to which community trajectories can be influenced by management through the founding community, stocking, connectivity of the ecosystem, and/or species removal remains unclear (Matthews and Marsh-Matthews, 2016; Milner et al., 2011; Vander Zanden et al., 2006). While the overall productivity of a set of species of interest is one metric of interest (and central to Canadian policy), producing an offset ecosystem with similar species diversity to a majority of natural systems has the potential to provide comparable resilience, health and function in the ecosystem (Bull et al., 2013; Dudgeon et al., 2006; Lambeck, 1997). Thus, under scenarios where habitat offsetting is not a 'like-for-like' replacement, ecological equivalence between pre-existing ecosystem and its offset ecosystem may be maximized by using species diversity targets alongside productivity targets (Bull et al., 2015; Bull et al., 2013).

Using a long-term data set (2008–2015) from the first compensation lake in the oil sands, we found that fish communities were significantly changing and declining in mean trophic level through time. Moreover, we demonstrate that fish (less connected) and benthic invertebrate (more connected) communities are not concordant, suggesting that the founding fish community and reduced connectivity for fish species may have had a significant and strong impact on the community assembly process. Of note, the continued low connectivity of fish community likely inhibits the expected trend found in more natural ecosystems, where later stage species additions or migrations of large-bodied predators are expected soon after the establishment of potential prey species (Vander Zanden et al., 2006). Specifically, we determine that increases in the abundance of two species, Longnose sucker and White sucker, largely contributed to the decline in mean trophic level. What is problematic with this outcome from the conservation perspective, is that the resulting fish community is uncommon within the broader region. The unbalanced trophic structure of the fish community also suggests that current trajectories of the fish community will likely create a less resilient ecosystem and less sustainable fishery over the long-term.

Management can undoubtedly influence the outcomes of establishing communities, especially when intervening with system connectivity (Carrara et al., 2012; Chase et al., 2009; Thompson et al., 2017). In this study, we highlight that the exclusion of top-down regulation for the fish community can have a significant and strong impact on the trajectory of fish communities. This has contributed to the discrepancy between the fish species found in Horizon Lake and the species pool within the vast majority of other lakes in the region. As multivariate approaches such as PCA can be sensitive to the presence/absence of species (Legendre and Legendre, 2012), the absence of later stage additions of top-predators (in the community assembly process) may also be contributing to the lack of a strong concordance between benthic invertebrates and fish communities. Specifically, we find that fish species diversity increased gradually over the course of this study, whereas the species diversity of benthic invertebrates in Horizon Lake increased more rapidly within the first couple of years after

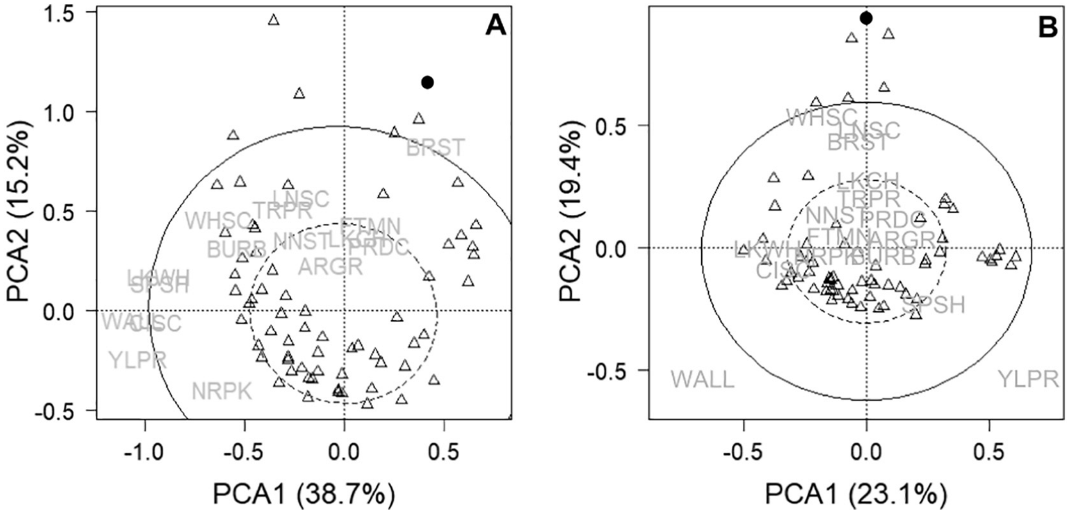

Fig. 5. Principal components analysis using (A) presence-absence of species from 102 lakes and (B) Hellinger transformed abundances from 66 lakes in the lower Athabasca region. Horizon Lake is represented by the filled circle and other lakes within the region by the open triangles. The solid and dashed lines denote the 95% and 50% confidence ellipses, respectively. Species codes can be found in Table S3.

impoundment. Benthic invertebrates demonstrate a different pattern than fish communities as they have increased connectivity, because most benthic invertebrate species have some ability to move over land into new ecosystems (Mackay, 1992). In some instances when restored or newly created ecosystems are well connected, fish species may also be able to disperse to the new ecosystem (Milner et al., 2011; Scrimgeour et al., 2014); however, when the new system is not connected to species pools representative of pre-existing ecosystems, facilitated migration could also be used to establish desirable fish species (McLachlan et al., 2007). In the case of our study system, facilitated migration (or stocking) was not implemented. Benthic invertebrates support fish communities within the food web, so it would be anticipated that there is some concordance between fish and benthic invertebrate communities within our study (Jackson and Harvey, 1993). Here we do detect a potential trophic link between invertebrates and fish, with successive peaks in abundance, respectively, but compositional patterns show non-concordance and a mismatch between the two taxonomic groups.

Higher trophic level fish species (e.g., Northern Pike (*Esox lucius*), Lake Whitefish (*Coregonus clupeiformis*) and Burbot (*Lota lota*); Table 1 and Table S1) are absent in the compensation lake, suggesting that potential top-down control in the fish community that could be in the lake is absent (Brashares et al., 2010; Carpenter et al., 2001; Estes et al., 2011). Allowing predators to establish (by increasing connectivity or facilitating establishment) could have added benefits of introducing a top-down control, which increases functional diversity and resilience in the fish community (Chase et al., 2009; Dudgeon et al., 2006; Vander Zanden et al., 2006). Moreover, top-down structuring may be desirable within the ecosystem during the initial establishment of fish communities as a common phenomenon to reservoir type lakes is an initial nutrient release that provides bottom-up structuring of the food web (Carpenter et al., 2001; Grimard and Jones, 1982; Kinter and Ludsin, 2013). Both a nutrient release that increases resources for fish species (bottom-up) and the absence of predators that reduces predation (top-down) can together combine to produce increases in the abundance of lower level trophic species that have already established in the lake (Brashares et al., 2010; Carpenter et al., 2001; Estes et al., 2011; Kinter and Ludsin, 2013). We found that fish abundance increased in the compensation lake over the first 8 years and this was primarily driven by two detritivore species, Longnose sucker and White sucker (Fig. 2A and Table 1). Common predators of these sucker species were absent in the compensation lake (Barton, 1980; Nelson and Paetz, 1992), which reduces predation pressure and allows mechanisms such as meso-predator release to occur (Brashares et al., 2010; Carpenter et al., 2001). Additionally, the diets of both of these sucker species are made up of highly abundant resources in the compensation lake such as detritus, algae and benthic invertebrates, which indicates that resources are not limiting (Barton, 1980; Nelson and Paetz, 1992). While this might lead to a dramatic increase in abundance and productivity, after reaching carrying capacity we might expect a subsequent steep decline in abundance of these detritivores (Table S1). Our study suggests that there may be a high degree of variability in fisheries productivity, which is related to the absence of top-down regulation. In turn, we assert that these findings imply that the compensation lake ecosystem will likely have high variability in fisheries productivity in its current form.

4.1. Reconciling management objectives

Fish species composition and decreases in mean trophic level in the compensation lake are a direct result of the management practices that have been put in place. From a species-specific perspective, Alberta has seen strong declines in Arctic Grayling, designating it a sensitive species within the province and making it a potential focus of the management strategy for the compensation lake (ASRD, 2005). From a lake or ecosystem perspective, there is a desire to replace lost fisheries productivity supported by the newly created fish habitat in the compensation lake at a replacement level of at least twice the amount of productivity that previously existed on the unaltered landscape (Minns, 2015; Rice et al., 2015). Currently, it can be stated that these management objectives have been met for the habitat offset, however, maximizing the productivity of an individual species and all species, appears to be in conflict and there are also many uncertainties.

Arctic Grayling abundance has shown a steady increase in the compensation lake over the last 8 years. This increase in Arctic Grayling abundance in the compensation lake is likely attributable to the provisioning of new habitat and a reduction in potential predation. The compensation lake is also relatively deep for this region (maximum depth of 23 m) and may provide good quality over-wintering habitat. Increased survival and productivity in deeper boreal lakes may be achieved by reducing the frequency and intensity of energetic bottlenecks, where fish are faced with reduced resources and physiologically stressful abiotic conditions (e.g., low temperature, low dissolved oxygen) during winter (Shuter et al., 2012). However, despite this understanding, there is a need to empirically quantify the potential impact of winter conditions on the productivity of Arctic Grayling and other species in the boreal region. As one reason why Arctic Grayling are not common within lakes in the lower Athabasca region may be that deeper lakes (which can act as winter refuges) are also not common.

By also excluding, to date, large-bodied predators (e.g., Northern Pike) (Tonn et al., 2004) this has facilitated some increases in Arctic Grayling productivity within the compensation lake, but also limits other potential sources of fisheries productivity and the resilience these predators might confer across the food web (Chase et al., 2009). Moreover, despite some increases in Arctic Grayling abundance, it is still not clear how higher trophic level species may compete with Arctic Grayling (i.e., niche partitioning) and/or potentially increase predation pressure (Stewart et al., 2007). Nonetheless, the outcome of not facilitating the establishment of large bodied predators has created fish communities that are not common to most lakes within the region.

Lastly, the long-term management plan (30 + years) is to reconnect Horizon Lake to the Athabasca watershed, where Northern Pike are abundant and could likely colonize. At this time frame, increasing the connectivity of the compensation lake would allow Northern Pike to be introduced to prey that are naïve to predators, where many prey species would face population declines (Berger et al., 2001; Martin, 2014). The introduction of large-bodied predators at this late stage of community assembly will likely destabilize species interactions and food webs, increasing the uncertainty associated with long-term productivity and species diversity within the ecosystem.

While a single species approaches such as promoting Arctic Grayling productivity as a form of habitat offsetting may from the outset appear to be more certain, there are several uncertainties that can arise from single species management approaches (DeFries and Nagendra, 2017). In particular, this might include the influence of energetic bottlenecks during winter that reduce productivity, reduced ecosystem resilience due to lower redundancy and diversity of species present, and impacts to the long-term stability of the fish community due to late stage species introductions. One exception may be scenarios involving umbrella species, whereby protecting a single species can indirectly protect many other species that can be found within its preferred habitat (Lambeck, 1997). In our study, we find that the species composition in the compensation lake is uncommon throughout the region, which may produce an ecosystem with decreased resilience and function, because Arctic Grayling by all appearances are not an umbrella species. On the other hand, it should be noted that creating a rare community and ecosystem may have an added benefit of increasing the productivity of a desirable rare species within the region, where the habitat offset can act as a refuge in the face of broad scale changes to climate and land-use (ASRD, 2005; Poesch et al., 2016). However, given the spatial and temporal scale of stressors there are also uncertainties and concerns regarding the long-term viability of Artic Grayling populations within a refuge like the compensation lake in this study.

4.2. Reference systems and conservation targets

Determining an appropriate reference system and baseline for habitat offsets, such as compensation lakes, can be a nontrivial task. Differences in the fish community between lotic and lentic ecosystems are difficult to reconcile, as differences may result from the different processes that are at play (e.g., predator release, nutrient release), connections with larger systems (e.g., Athabasca River) or simply that we have different sets of species found between these systems (Johnson et al., 2008; Rahel, 2002). The different sets of species found in lotic and lentic ecosystems, highlights one of the major difficulties with selecting reference systems for compensation lakes, as the ecosystems would confer different levels of productivity and diversity. Moreover, the establishment of a baseline or reference for habitat offsetting is also challenging given changing and ongoing development across the landscape (i.e., a control or reference site would be in flux due to ongoing human activities) (Kopf et al., 2015).

One way to circumvent these issues is to use regional wide metrics for management targets, such as productivity, diversity and habitat. Having these multiple management targets may help to produce more desirable levels of resilience, health and function in ecosystems (Dudgeon et al., 2006; Lambeck, 1997; Tilman et al., 1997). In this study, we highlight that the species assemblage and composition in Horizon Lake is not common to most lakes within the lower Athabasca region. Thus, if the species assemblage in a habitat offset is not common, this implies that the sources of fisheries productivity (which is a management target) are different from other lakes within the region. This raises some concern that the fisheries productivity in the compensation lake may not be sustainable given the potential for lower ecosystem resilience and function due to a reduced mean trophic level and uncommon species community. This also highlights the need to better understand productivity-diversity relationships within freshwater ecosystems (Hooper et al., 2005). Moreover, this can be extended to consider functional diversity, where increased diversity (or redundancy) across functional guilds may confer higher levels of ecosystem resilience (McCann, 2000). Lastly, where needed, we suggest to incorporate measures of diversity alongside productivity and habitat metrics into offsetting practices. This can prove beneficial as diversity is related to important ecosystem attributes such as resilience and function (Dudgeon et al., 2006; Lambeck, 1997; Tilman et al., 1997) and productivity conveys the state of populations and/or communities within an ecosystem (de Kerckhove, 2015). Together these metrics could increase the long-term prospects of habitat offsets.

5. Conclusions

This study demonstrates that there can be a large degree of determinism in the community assembly process, meaning that management can have a strong and significant influence on the trajectory of a recently established fish community. Here the creation of the compensation lake with a maintained low level of connectivity and a founding fish community that has an absence of large-bodied fish predators, has likely improved the prospects for Arctic Grayling productivity. Under current policies and management objectives, both overall productivity and single-species targets have been achieved. However, this outcome has resulted in an ecosystem where the majority of the fisheries productivity can be found in lower trophic level species, not the focal species, Arctic Grayling. Unfortunately the absence of any notable top-down regulation on the fish community, will produce large oscillations in abundance of lower trophic level species, implying that productivity based management targets may not be sustained over the long-term (Carpenter et al., 2001; Chase et al., 2009; Yang et al., 2008). This reinforces the need to incorporate diversity based targets into habitat offsetting practices to produce offsets with a more balanced trophic structure, species assemblage and productivity that is likely to be sustainable over the long-term. Ideally, this includes promoting diversity comparable to pre-existing and nearby ecosystems (i.e., ecological equivalency) alongside productivity targets. This framework can provide a better opportunity to establish sustainable, resilient, healthy and functioning ecosystems and produce habitat offsets that are more ecologically equivalent.

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Appendix A. Supplementary data

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