Establishment, spread and impact of Prussian Carp (*Carassius gibelio*), a new invasive species in Western North America

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Abstract

Freshwater ecosystems are some of the most imperilled on the planet. Invasive species pose the second largest threat to freshwater organisms after habitat degradation. Aquatic introductions have led to extinctions, competition for resources, hybridization, the introduction of foreign pathogens and the alteration of ecosystem structure and function. One of the most recent invaders in western North America is Prussian Carp (*Carassius gibelio*). The first record of this species in North America was in 2000, in Alberta, Canada, yet little is known about its invasion, current distribution or effects on stream communities. In Eurasia, Prussian Carp have been assessed as one of the most harmful invasive fish species because of its ability to reproduce asexually, high environmental tolerances and preference for human modified habitats. The arrival of Prussian Carp in western North America poses concerns for many native freshwater species. Therefore, the objectives of this study were to assess the severity of Prussian Carp's invasion in western North America by 1) mapping Prussian Carp distribution and rate of spread since its initial arrival; 2) analysing the impact of Prussian Carp on native fish species; and 3) identifying environmental parameters that predict Prussian Carp presence. Using kernel density functions, we found that the range of Prussian Carp increased in Alberta, Canada from approximately 500 km² since its arrival (estimated as 2000) to over 20,000 km² in 2014. The rate of spread is increasing at an exponential rate over five year increments (e.g. 1.6, 2.1, and 2.3 times), suggesting rapid expansion since first detection. Our results did not indicate that Prussian Carp have a negative effect on native fish species, which is likely due to its recent expansion into these areas and an already depauperate species community. The most important habitat variables that best predicted the presence of Prussian Carp were: dense aquatic vegetation, high conductivity, pH, high dissolved oxygen and low flow rates indicating preference for relatively

slow, eutrophic streams. Successful management of this species in western North America will require the integration of all levels of government between neighbouring provincial and national borders, as well as the public. Prussian Carp are a highly mobile species and given the connection to other watersheds in Canada and proximity to the Missouri/Mississippi drainages in the United States, agencies throughout North America should be aware of this invasive species and the potential impacts on native biota.

Preface

This thesis is original work by Cassandra Docherty. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, under Stream Assessment, No. Au0000757.

Chapter 3 of this thesis was written for publication as C. Docherty, K. Hamilton, K. Neufeld, L. Macpherson, A. Hamann, J. Ruppert and M. Poesch, "Establishment, spread and impact of Prussian Carp (*Carassius gibelio*), a new invasive species in western North America". The study was conceived by my supervisor Mark Poesch and I led the analysis and wrote the first draft of the manuscript. My co-supervisor Andreas Hamann helped with the analysis. Kenton Neufeld and Kyle Hamilton assisted with data collection. Laura Macpherson contributed additional data, and Jonathan Ruppert provided statistical support and advice. All authors contributed manuscript revisions and edits.

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Chapter 1 : Introduction

Freshwater ecosystems are some of the most imperilled on the planet (Leidy & Moyle, 1998; Ricciardi & Rasmussen, 1999; Dudgeon *et al.*, 2006). In North America, aquatic habitats experience widespread degradation from anthropogenic activities (Dudgeon *et al.*, 2006). In the last century, degradation has been so prevalent that 40 percent of all fish taxa are considered imperilled and 61 freshwater species have gone extinct (Ricciardi & MacIsaac, 2000; Jelks *et al.*, 2008). Historically, aquatic habitats in North America were home to the largest diversity of temperate fish, mussels and crayfish in the world (Williams *et al.*, 1993; Taylor *et al.*, 1996; Abell, 2000). Now, extinction rates are five times higher than terrestrial environments and rival those of tropical rainforests (Ricciardi *et al.*, 1998; Ricciardi & Rasmussen, 1999). Aside from habitat degradation, invasive species pose the second largest threat to freshwater fauna in North America (Jelks *et al.*, 2008). Aquatic invasions have led to extinctions (Lowe *et al.*, 2000), competition for habitat and resources (Hill & Lodge, 1999), the introduction of pathogens (Youngson *et al.*, 1993) and habitat alteration (Parkos III *et al.*, 2003). Furthermore, the disruption of aquatic environments from invasive species can change the structure and function of ecosystem processes and result in trophic cascades (Elmqvist *et al.*, 2003).

An invasive species is defined as an "*alien species which threaten ecosystems, habitats or species or is likely to cause economic or environmental harm or harm to human health*'' (Clinton, 1999; Center for Biological Diversity, 2001). Therefore, under this definition, it is possible to have an established non-native species that does not demonstrate invasive qualities (Gleditsch & Carlo, 2011). Indeed, a species must overcome multiple logistical, physiological and biological limitations before it can become invasive. These limitations have been broken down into multiple phases: transport, release or escape, establishment, spread and impact with each phase having its own specific set of mechanisms that govern survival (Kolar & Lodge, 2002; Hellmann et al., 2008)(Fig. 1). For instance, during transportation a species has to remain viable with enough individuals to establish a population in a new environment (Fig. 1a) (Mack *et al.*, 2000). The number of individuals or number of times a species is introduced into a new location (i.e. introduction effort) can play a large role in determining the likelihood of establishment and proliferation of a species (Lodge, 1993). Once a species reaches a new environment it will encounter a number of novel stresses (i.e. climate, environmental conditions, biotic interactions, etc. (Sakai et al., 2001; Shea, 2002)) that will likely hinder its survival; however this may be offset by the relief from native predators and co-evolved pathogens, aptly termed "the enemy release hypothesis" (Keane & Crawley, 2002). Other factors that will determine a species establishment (Fig. 1b) and spread (Fig. 1c) and eventual impact (Fig. 1d) once it reaches a new environment include its ability to persist under a wide range of environmental conditions, climatic compatibility, biological interactions and the available niche space in an ecosystem (Blackburn & Duncan, 2001; Keane & Crawley, 2002; Shea, 2002). Furthermore, species specific traits such as high fecundity, early age at maturity, asexual reproduction and large dispersal ability will help a species become established and spread (Lodge, 1993).

To assess the invasion potential of a species, it is important to know how far and how fast it can spread once it becomes established. Dispersal ability is one mechanism responsible for the spread of an invasive species and has been noted as an essential component of aquatic invasions (Rehage & Sih, 2004). Dispersal is defined as a one way movement from one site to another, which is influenced by a species behavioural characteristics at different life stages (Lidicker Jr & Stenseth, 1992; Rehage & Sih, 2004). At a broad spatial scale, the ability of a species to disperse through a watershed will depend on connectivity (Hitt & Angermeier, 2008). In North America, drainage basins have been both fragmented through the construction of dams, weirs, and improper installation and maintenance of stream crossings and augmented through drainage canals built for agriculture and transport (Pringle, 2003; Rahel, 2007; Bourne *et al.*, 2011). Instream barriers have led to the loss of connectivity and fragmentation of waterways, which hinders the spread of invasive species (Pringle, 2003). On the other hand, canal systems have increased connectivity by allowing invasive species to circumvent natural dispersal barriers (i.e. catchment boundaries) and colonize previously inaccessible habitats, leading to accelerated rates of spread (Pringle, 2003; Post *et al.*, 2006; Rahel, 2007).

Biological and behavioural traits can also determine a species ability to disperse and spread. Life history traits such as asexual reproduction, high fecundity and early sexual maturity appear to be a prerequisite for becoming a successful invader (Lodge, 1993; Sakai *et al.*, 2001). These specific life history characteristics allow populations to reach high densities in a short amount of time, leading to density-dependent dispersal to avoid competition for resources and habitat (Post *et al.*, 1999). Further, evidence suggests that a species behaviour can determine its dispersal ability and rate of spread (Cote *et al.*, 2010). Personality-dependent dispersal occurs in species that are more daring, aggressive or territorial, and anti-social (Cote *et al.*, 2010).

Other factors that enhance the spread of aquatic invasive species are the proximity to urban centers and human influence. Indeed, there is a higher probability of species movement and establishment closer to urban centers than in remote locations from increased angler density and interaction with aquatic ecosystems (Jenkins & Burkhead, 1994; Nico & Fuller, 1999). The frequent interaction with aquatic habitats often leads to intentional or unintentional human-assisted dispersal of aquatic organisms through bait fishing, stocking, improper cleaning of water vessels and other equipment, and aquarium release (Jenkins & Burkhead, 1994; Lintermans, 2004; Rahel, 2007). In addition to the physical movement of species, humans also influence habitat quality. Aquatic ecosystems that are degraded from human activities are considered to be more susceptible to invasive species than pristine habitats (Ross *et al.*, 2001; Dudgeon *et al.*, 2006). This is because human caused disturbance can disadvantage native communities by changing the historical supply and acquisition of resources, weakening ecosystem function (Sher & Hyatt, 1999; Shea, 2002). Invasive species, on the other hand, are typically habitat generalists and have broad environmental tolerances, thus are better equipped to withstand conditions that may be unfavourable to native species (Marvier *et al.*, 2004). This can result in invasive species outcompeting native species or exploiting new niches in unsuitable habitat, further facilitating its invasion (Keane & Crawley, 2002; Shea, 2002).

Underlying the success of an invasive species in a newly colonized environment are other ecological concepts such as ecological niche. An ecological niche, which is described as the spatial and temporal affiliation of an organism and the biological and physical components of a habitat, will play a role in the establishment and spread of an invasive species (Shea, 2002). Available niche space in an ecosystem will depend on resource availability (i.e. the supply of resources from the surrounding environment and how efficient the local community is at reducing those resources) and how well an invasive species can exploit those resources, the type of predators (i.e. specialist or generalist predator) and abiotic conditions (i.e. climate, water availability, etc.) (Shea, 2002). In theory, species in mature, more diverse communities will have had a longer time to adapt to local conditions and exploit all available habitat niches than young communities, and thus, mature ecosystems should be more resistant to invasion (Petchey & Gaston, 2002). However, this is a simplified understanding and empirical evidence has demonstrated a few examples where mature, highly diverse communities have been invaded multiple times and young communities have resisted species invasions (Baltz & Moyle, 1993; Hall & Mills, 2000). This is because an invasive species, may in fact, be more efficient at securing resources from the environment than a native species, have less resource requirements overall, or be a superior competitor to a native species that currently occupies the ecological niche (Shea, 2002). The type of predator will be important for regulating the spread of invasive species by increasing mortality and restricting feeding efficiency (Shea, 2002). If an ecosystem is occupied by specialized predators that have evolved with a specific type of prey, then the regulation of the invasive species will likely be poor (Torchin *et al.*, 1996). However, generalist predators may be better at controlling invasive species as they don't have the same prey restraints (Shea, 2002). Additionally, the interaction with the abiotic environment will determine the survival of an invasive species (Moyle & Light, 1996a). The likelihood of survival and establishment will increased if the abiotic environment provides comparable conditions to that of an invasive species home range (Moyle & Light, 1996a).

In North America, most aquatic ecosystems are relatively young, geologically and evolutionarily speaking (i.e. < 10, 0000 years old), and species richness tends to range from low to moderate (Prentice *et al.*, 1991; Allan & Flecker, 1993). In accordance with the ecological niche theory, this would suggest an insufficient amount of time for speciation or for current assemblages to exploit all available habitat niches (Shea, 2002). This is not to say that these systems do not have a high level of endemism. Freshwater species in North America have moderate to high endemism because of the degree of isolation between drainages (Allan & Flecker, 1993). It is the combination of vacant niches and endemic fauna that makes the aquatic habitats of North America vulnerable invasive species. This has been demonstrated by the increase in species invasions in the last few centuries (since post-European colonization) that have resulted in extensive changes in species composition (Gido & Brown, 1999).

One of the most recent introductions to western North America is Prussian Carp (*Carassius gibelio*). This species was introduced to streams in Alberta, Canada, in the year 2000 (ESRD, unpublished data). Prussian Carp are a species native to Asia but have been introduced to Europe where they occupy both natural and artificial waterways from the Baltic Sea to the Mediterranean and from the United Kingdom to Russia (Vetemaa *et al.*, 2005; Tarkan *et al.*, 2014). Prussian Carp exhibits a variety of biological and behavioural traits linked to its invasional success. Firstly, Prussian Carp reproduces asexually through a process called gynogenesis which utilizes the sperm of other cyprinids to activate the development of the egg but contributes no genetic information, leading to populations of clonal, triploid females (Gui & Zhou, 2010). Prussian Carp is also renowned for its competitive behaviour, particularly when populations reach high densities (Kalous *et al.*, 2004; Gaygusuz *et al.*, 2007). These two traits in addition to its preference and tolerance for human modified habitats has made it one of the most successful invaders in Eurasia (Perdikaris *et al.*, 2012). In North America, particularly in the Great Plains region where Prussian Carp have been found, aquatic habitats have become degraded on account of anthropogenic activities such as agriculture, providing suitable habitat for this species (Dodds *et al.*, 2004). This region also has an extensive network of canals that will allow Prussian Carp to breach historical watershed boundaries with ease (Post *et al.*, 2006). Although fish species in northern habitats are relatively hardy due to climatic and hydrological variability, anthropogenic influences have reduced native species richness in these communities in recent decades (Matthews, 1988). This may present an opportunity for Prussian Carp to fill a vacant niche that was once occupied by a native species. Alternatively, Prussian Carp's competitive nature and environmental tolerances may make it a better competitor than a species that currently fills that ecological niche, leading to niche displacement and a decline in native species.

There may be a few limiting factors of Prussian Carp invasion in North America. Prussian Carp are likely intentionally imported as live specimens and therefore they must survive prolonged periods of containment prior to being released in their new environment. Once Prussian Carp is released into freshwater systems of North America its survival, establishment and spread will depend on its ability to adapt to the highly variable climatic and hydraulic conditions of the Great Plains Region. The Great Plains region has a continental climate characterized by temperature extremes and intermittent seasonal fluctuations in hydrology (Matthews, 1988). In some of the more arid regions, lower order tributaries may experience periods of prolonged drying where refugia are limited, whereas larger river systems are subjected to frequent flooding (Dodds et al., 2004). Unfamiliarity with local hydraulic regimes and temperature extremes would likely lead to higher morality of Prussian Carp. If resources and habitat are limited in freshwater systems where Prussian Carp are introduced, then biotic exclusion from native species may help prevent Prussian Carp establishment and spread. In addition, the presence of predators may help prevent Prussian carp establishment, as well as population regulation as it spreads (Vetemaa et al., 2005). Moreover, if available spawning partners (i.e. native Cyrpinids) are scarce in this region this will also reduce Prussian Carps ability to establish and spread.

Thesis objectives

Prussian Carp have been in North America for 15 years, yet little is known about its invasion, current distribution or effects on stream communities. The objective of this research is to address knowledge gaps of Prussian Carp's invasion and assess the invasion severity in western North America. Chapter two provides an extensive literature review on Prussian Carp in Eurasia to assess the risk this invasion poses to freshwater fishes in western North America. Chapter three presents Prussian Carp's current distribution in western North America, investigates the impact to local fish communities and highlights habitat variables that best determine Prussian Carp's presence in Alberta. Lastly, feasible management strategies to control Prussian Carp in western North America are discussed in chapter four.

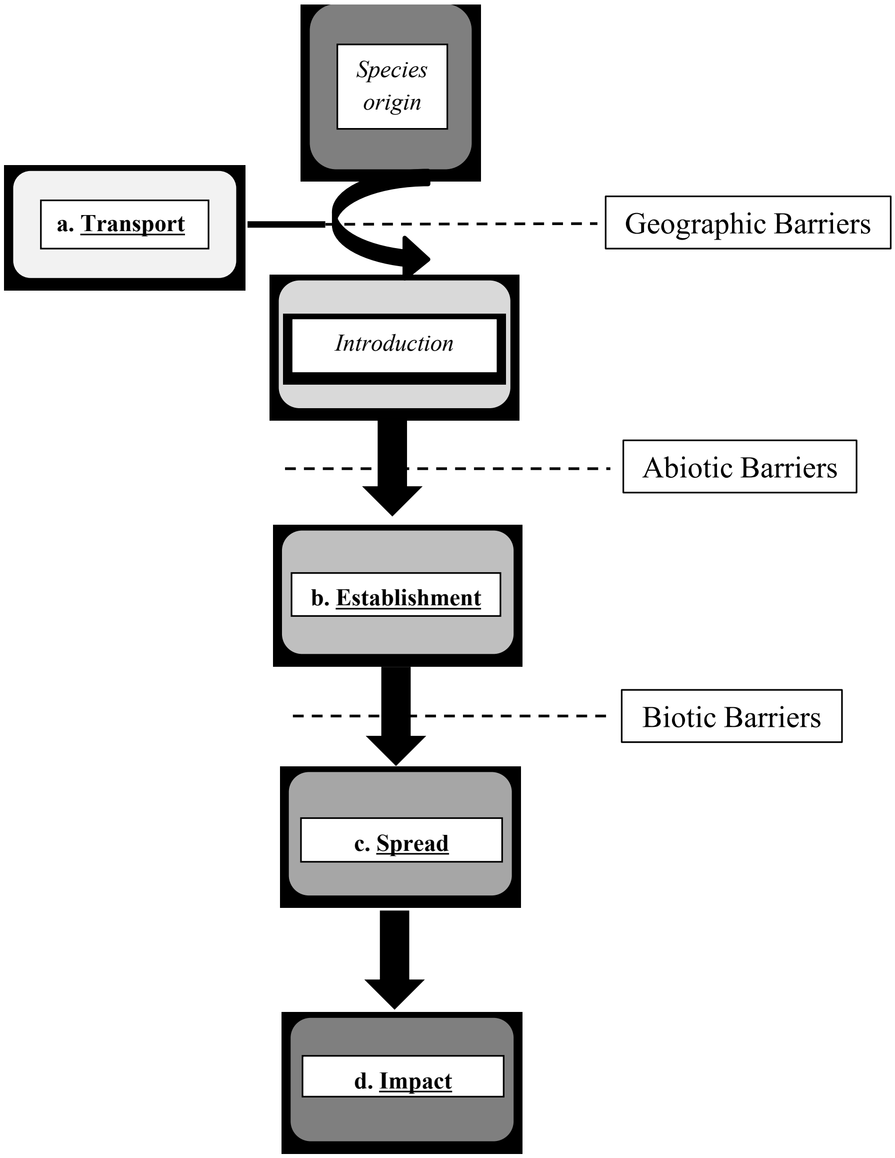

Figure 1 - The stages of a species invasion adapted from Hellman *et al.* 2008. Stages include: transport and introduction, establishment, spread and impact. A species must overcome multiple physical, abiotic and biotic barriers before it becomes an invasive species.

Chapter 2 : Assessing the potential impact of Prussian Carp to freshwater fishes in North America: A review

Introduction to invasive species

Humans have been moving species, particularly cultivars, livestock and other trade items, outside their natural geographic boundaries for millennia (DiCastri, 1989). In the last 200 years, globalization has led to an unprecedented increase in the number of species introduced into foreign environments (DiCastri, 1989). Currently, species are purposefully moved outside their natural range for recreational fisheries or game reserves, biological control, pet trade, and sustenance (Strayer *et al.*, 2006; Gherardi, 2007; Hellmann *et al.*, 2008). One of the largest unintentional movements of species comes from trade and commerce. Oceanic vessels release organisms through ballast water discharge or as "hitch hikers" attached to the external haul of the ship (Moyle & Light, 1996b; Dextrase & Mandrak, 2006). When a species is released into a new environment there is a chance it can establish and become invasive (Williamson, 1996). Indeed, it is estimated that 3% of the earth's ice free surface is occupied by invasive species (Mack, 1996). At present, invasive species inhabit nearly every biome on the planet, even some of the most remote places like Antarctica (Frenot *et al.*, 2005). The general consensus within the scientific community is that invasive species pose a severe threat to native species and their respective ecosystems, and are one of the primary reasons for biodiversity loss around the world (Vitousek *et al.*, 1996; Rahel, 2000).

Some ecosystems, like islands and freshwater, appear to be more vulnerable to species invasions because of the degree of isolation and level of endemism (Lodge, 1993). Aquatic ecosystems, in particular, have an increased susceptibility to invasive species because they are often degraded from anthropogenic activities such as chemical runoff, acidification, disruption of natural hydrology, overfishing and climate change (Gurevitch & Padilla, 2004; Millennium

Ecosystem Assessment, 2005; Dudgeon *et al.*, 2006; Hellmann *et al.*, 2008). These activities interact synergistically leading to a weakening of ecosystem structure and function (Elmqvist *et al.*, 2003). It is generally accepted that degraded habitats are more likely to succumb to biological invasion than pristine habitats (Ross *et al.*, 2001). In fact, non-native aquatic species richness has been positively correlated with intensity of human disturbance (Whittier & Kincaid, 1999). In North America, invasive species pose the second highest threat to aquatic fauna next to habitat degradation (Jelks *et al.*, 2008). The frequency of human interaction with aquatic systems increases the likelihood of a species being introduced through human-mediated dispersal (Jenkins & Burkhead, 1994). Aquatic invasive species are most commonly introduced through accidental bait fishing release, improper cleaning of boats and other shipping vessels (i.e. via ballast water), stocking fisheries, release of aquaria species and escapement from aquaculture (Moyle, 1995; Hellmann *et al.*, 2008). Moreover, aquatic species, in general, have a higher probability of establishment than many terrestrial organisms (Williamson & Fitter, 1996; Ricciardi & MacIsaac, 2000; Jeschke & Strayer, 2005). This is demonstrated by Ruesink (2005) who found that 64% of fish species intentionally introduced since the mid 1800's became established in their new habitats, and 22% of those establishments had negative effects on the local ecology.

The invasion of Prussian Carp

Prussian Carp are one of the most successful and harmful invasive fish species in Eurasia (Kalous *et al.*, 2004). They are a Cyprinid species native to Asia but were introduced to Europe in the 1600's, and through migration, intentional or accidental introduction, its distribution now extends from Scandinavia to the Mediterranean and from the United Kingdom to Russia (Povž & Šumer, 2005). Identification of Prussian Carp in new habitats has been challenging because they are morphologically similar to other *Carassius* species such as Crucian Carp (*Carassius carassius*), the Goldfish (*Carassius auratus*), *Carassius langsdorfii,* and *Carassius curieri* (Aydin *et al.*, 2011). In Eurasia, Prussian Carp are often wrongfully identified as native Crucian Carp (*Carassius carassius*) leading to delayed detection in some regions. This morphological similarity has led to accidental stocking with Crucian Carp and other Carp species, facilitating its spread throughout Eurasia (Aydin et al., 2011). Misidentification of Prussian Carp for the Goldfish in prairie streams of western North America has likely led to its delayed detection and management response. The first record of Prussian Carp was in Alberta, Canada, in the year 2000, but it wasn't until 2014 that it was officially genetically confirmed (Elgin *et al.*, 2014). Prussian Carp's inherent invasive qualities and negative effects on the local ecology in regions throughout Eurasia raise concerns about its presence in North America (Kalous *et al.*, 2004). To assess its invasion potential and effect on local fish species in North America, it is imperative to understand Prussian Carp's biology and life history traits, and what mechanism have led to its invasion success in Eurasia. Hopefully this will in turn provide insight on the effects to local fish species in western North America and guide management decisions in the future.

Biological and life history traits of Prussian Carp

Prussian Carp displays a type of asexual reproduction called gynogenesis that is most prevalent in newly established populations (Tarkan *et al.*, 2012a). This reproductive method utilizes the sperm of related species (i.e. other cyprinids) to activate the development of the egg but contributes no genetic information to the offspring (Gui & Zhou, 2010). The progeny from gynogenetic reproduction are clonal, triploid females, identical to their mother. In populations where triploid females are dominant, males do exist but at very low frequency and often are triploid or tetraploid (Liasko *et al.*, 2010). Some triploid female populations have diploid males, but Vetemaa *et al.* (2005) found that most males had stunted gonadal development and therefore did not significantly contribute to reproduction. Until relatively recently, diploid populations only existed in Eastern Asia, but regions of Ukraine and Russia have started seeing the transition from triploid to diploid, which might indicate that time since establishment can influence the sex ratio of Prussian Carp populations (Abramenko, 2011). One example is from the River Danube where Prussian Carp populations were initially dominated by triploid females but within a decade transitioned to sexually reproducing diploid populations (Aydin *et al.*, 2011). Interestingly, where triploids were present, population were always skewed towards females, but where triploids were absent, the sex ratio was 1:1 (Liasko *et al.*, 2011).

In order for gynogenetic reproduction to be successful, triploid females need to overlap spatially and temporally with other cyprinids during the spawning season (Tarkan *et al.*, 2012a). Maladaptation to local hydrological regimes and geochemical cues can lead to mismatches in spawning times between Prussian Carp and native congeners (Abramenko, 2011). Indeed, this was the case for Prussian Carp and Common Carp in the Ponto-Caspian region leading to multiple failed spawning attempts (Abramenko, 2011). Documented spawning time and duration for Prussian Carp varied quite dramatically throughout Eurasia and is likely dependent on multiple factors including suitable habitat, available spawning partners, environmental stochasticity and latitude (Munro *et al.*, 1990). The earliest spawning times recorded were in April and the latest were in August, with the water temperatures ranging from 14°C – 29°C (Şaşi, 2008). Analysis of oocytes (egg development) confirms that Prussian Carp are capable of spawning multiple times a year and the number of eggs per female can range from 30,000 to 250,000 (Şaşi, 2008). Age at maturity for this species is typically between one and three years and the average life expectancy is 6 years, with a maximum age recorded of 11 years (Banarescu

& Paepke, 2001). Prussian Carp, like many invasive species, exhibit rapid growth at a young age affording them a competitive advantage over native species (Stearns, 1976). One disadvantage to reproducing asexually is the vulnerability to pathogens and parasites. There is some evidence that clonal species have a limited tolerance for parasites and disease from reduce genetic variability, which may be the case for Prussian Carp (Hakoyama *et al.*, 2001). Lake Řěhačka in the Czech Republic experienced a mass mortality of Prussian Carp from the cyHV-2 cyprinid herpes virus. No other species appeared to be affected and all specimens that were collected were triploid females (Daněk *et al.*, 2012).

Aside from Prussian Carp's reproductive strategy, they are known as an aggressive competitor and a voracious eater (Gaygusuz *et al.*, 2007). Prussian Carp are an omnivorous species whose diet consists of phytoplankton, zooplankton, benthos, detritus and macrophytes (Specziár *et al.*, 1997; Balik *et al.*, 2003). Throughout the literature, Prussian Carp's diet changed depending on the season, habitat (e.g. lake vs. river vs. artificial habitat) and life stage. In Lake Eğirdir, Turkey, the gut contents of Prussian Carp were predominantly plankton and benthic invertebrates, with the most dominant orders including dipterans, copepods, gastropods, cladocerans, and ostracods (Balik *et al.*, 2003). *Daphnia* (cladoceran) occupied the highest percentage of gut contents overall, but the proportion of species changed over the year. Gastropods dominated the gut contents in the spring, cladocera in the summer and autumn, and Diptera in the winter. Other studies from lakes in Turkey found that only 30 percent of the diet came from invertebrates and the remainder came from aquatic plant species (Yılmaz *et al.*, 2007).

Prussian Carp are also considered a robust species, known for colonizing and thriving in a variety of environments. Habitat preferences include both natural and manmade waterways such as streams, rivers, canals, lakes, reservoirs, estuaries and ponds (Vetemaa *et al.*, 2005; Tarkan *et al.*, 2012b). Overall Prussian Carp have an affinity for slow moving or stagnant water. Streams with high gradients are not suitable for Prussian Carp and have been observed as a barrier to movement. For instance, upstream movement of Prussian Carp on the steep gradient of the Elbe River, Czech Republic, rarely surpassed 2 km, whereas downstream movement into the estuary reached 85km (Slavík & Bartoš, 2004). In the estuary, Prussian Carp displayed larger movements and home ranges in comparison to the main channel of the river (Slavík & Bartoš, 2004). To further exemplify Prussian Carp's weakness for steep gradients, there was only one Prussian Carp caught out of 10,000 fish in the fish ladders throughout this region. Additionally, Tarkan *et al.* (2012b) investigated life history characteristics of Prussian Carp populations between natural lakes, artificial waterbodies (ponds and reservoirs) and running water (canals, streams and rivers). Growth of Prussian Carp in natural lakes was the highest of all water bodies, whereas gonado-somatic index (i.e. gonad mass as a portion of total body mass) and fecundity were higher in artificial water bodies than streams and natural lakes. Additionally, artificial habitats also had lower age of sexual maturity, which may be a potential indicator of Prussian Carp's opportunistic life history traits. Other habitats preferences for Prussian Carp include eutrophic environments with submerged vegetation (Vetemaa *et al.*, 2005). Indeed, Liasko *et al.* (2011) found a positive correlation between the length-weight ratio and trophic state (i.e. higher phosphorus and nitrogen concentrations in the water yielded larger body sizes and a better condition index). Furthermore, In Ula, a manmade lake in Turkey, Prussian Carp were found in the high densities in areas with dense aquatic vegetation and had a higher condition factor than other species in the lake (Filiz *et al.*, 2011).

In addition to Prussian Carp's preference for eutrophic habitats, they can also survive under a variety of other environmental conditions intolerable to most fish species. For instance, Prussian Carp have a wide temperature threshold that ranges from 0°C to 30°C (Antonova, 2010) and can tolerate extremely low oxygen concentrations through metabolic depression, a process that is responsible for torpor and hibernation in other animals (Lushchak *et al.*, 2001). Remarkably, controlled experiments found that Prussian Carp can withstand ammonia concentrations upwards of 12.5 mg L^{-1} (pH 8.6) (Nathanailides *et al.*, 2003). This is compared to other freshwater fish where average acute toxicity occurs at 2.79 mg L^{-1} (pH 7.5) (United States Environmental Protection Agency, 1984). Prussian Carp's ability to tolerate unfavourable conditions is further exhibited during prolonged survival in cyanobacterial blooms (Perdikaris *et al.*, 2012). Prussian Carp can persist under these conditions because it shows high tolerance to intoxication by storing toxins in the liver and other tissues (i.e. ovaries, brain, intestine, muscle and kidneys) (Gkelis *et al.*, 2006; Kagalou *et al.*, 2008).

Impact of Prussian Carp in Eurasia

Prussian Carp's reproductive strategy, life history traits, diversity of habitat preferences, tolerance for adverse conditions and broad diet are all contributing factors to its invasion success (Kalous *et al.*, 2004). It has been noted that gynogenetic reproduction is one of the primary reasons for Prussian Carp's invasiveness because it allows it to become the most abundant species within a community in a short period of time (Tarkan *et al.*, 2012a). In order for this type of reproduction to be successful, Prussian Carp must rely on the sperm of related species for pseudo fertilization which ultimately leads to reproductive interference (Tarkan *et al.*, 2012a). Over time, reproductive interference will reduce the spawning success of native species likely leading to population declines (Tarkan *et al.*, 2012a). Indeed, Prussian Carp have been observed on the spawning grounds of other cyprinids and there is evidence of reproductive interference with native cyprinids in Turkey (Tarkan *et al.*, 2012a). Furthermore, when Prussian Carp do not utilize the sperm of related species for gynogenetic reproduction, they may be hybridizing with them. Papoušek *et al.* (2008) found that Prussian Carp were hybridizing with native Crucian Carp in Europe (*Carassius carassius*). Hybridization is major concern because it can dilute Crucian Carp's gene pool and endanger its genetic veracity, leading to a reduction in fitness or maladaptation to the local environment (Gross, 1998; Hänfling *et al.*, 2005).

Prussian Carp's prolific nature can be problematic when it comes to competition for resources with native and economically valuable species (Balik *et al.*, 2003; Gaygusuz *et al.*, 2007; Özcan, 2007; Şaşi, 2008). For instance, the introduction of Prussian Carp caused a decline and replacement of native Crucian Carp (*Carassius carassiu*s) in Russia, as they both occupy the same ecological niche in the ecosystems they coexist (Economidis *et al.*, 2000; Abramenko, 2011). Many other regions have observed declines in native cyprinids or trophic restructuring on account of Prussian Carp (Navodaru *et al.*, 2002; Balik *et al.*, 2003; Leonardos *et al.*, 2008a; Tarkan *et al.*, 2012a). In terms of competing with economically valuable species, Prussian Carp itself is of low economic value, but it is known to "clog" gillnets when fishing for economically desirable species (Zenetos *et al.*, 2009). In Lake Pamvotis, Greece, Prussian Carp became so abundant that they comprised 60% of the fish landed in 1998, while commercially valuable species simultaneously declined (Karipoglou & Pásenos, 2005; Leonardos *et al.*, 2008a).

As well, the ability of Prussian Carp to persist in degraded conditions gives it a competitive advantage over native species that are sensitive to disturbance (Leonardos *et al.*, 2008a; Liasko *et al.*, 2011; Tarkan *et al.*, 2012b). There is also evidence that Prussian Carp can degrade habitats and water quality in the systems it invades, further favouring environments where it can easily persist. For example, Prussian Carp was allegedly responsible for changing the nutrient cycle in the Kis-Balaton Reservoir (Paulovits *et al.*, 1998). Moreover, in Lake Mikri Prespa, Greece, Prussian Carp increased turbidity by disturbing sediment while foraging in the benthic areas, degrading water quality for native species (Crivelli, 1995). Lake clarity was further reduced by Prussian Carp's predation on zooplankton, which subsequently decreased grazing pressure on phytoplankton resulting in phytoplankton blooms.

Potential threats of Prussian Carp in western North America

Prussian Carp's establishment and spread in western North America presents concerns for the local aquatic community. Perhaps the most immediate effect on native species will be the consequences of reproductive interference from gynogenetic reproduction and competition for resources and habitat. Gynogenetic reproduction will likely reduce the spawning success of native cyprinids in western North America. There may be opportunities for Prussian Carp to utilize multiple sperm donors a year thereby substantially increasing its population size and facilitating its invasion. When Prussian Carp's population reaches a certain abundance it will likely overwhelm the system and ultimately lead to competition for habitat and food. There are 14 cyprinid species in Alberta, and 297 in all of North America, plus countless other species that overlap in diet and habitat preferences (Coker *et al.*, 2001). Therefore, the probability of population reductions, displacement or extinctions of prairie fishes potentially is high. While the risk of hybridization with native species in Alberta is low because are no documented cases of hybridization outside the Carp family, there are naturalized and introduced species of Carp (e.g. Common Carp (*Cyprinus Carpio*), Asian Carps (*Hypophthalmichthys nobilis and molitrix*), Grass Carp (*Ctenopharyngodon idella*), the Goldfish (*Carassius* auratus), etc.) throughout North America, which could have unpredictable consequences from genetic intermixing (Jerde *et al.*, 2013). Fortunately, the threat of Prussian Carp as a vector for pathogens and parasites also appears to be low because there are no documented incidences throughout its introduced range in Eurasia.

As for ecosystem impacts, prairie streams in North America are degraded from agriculture and other anthropogenic activities; therefore, it is uncertain whether Prussian Carp will have a significant influence on degrading water quality further. However, these degraded habitats may be what enable Prussian Carp to easily invade these systems. Many regions throughout Eurasia experienced habitat degradation in concert with Prussian Carp invasion, exemplifying their preference for these habitats (Paschos *et al.*, 2004; Perdikaris *et al.*, 2012). Prussian Carp have an affinity for eutrophic systems, particularly lakes, which would be prime habitat to colonize and potentially compete with native congeners (Slavík & Bartoš, 2004; Vetemaa *et al.*, 2005). Lakes in the Great Plains region of North America are exposed to effluence from agriculture and are often in a eutrophic state (Blais *et al.*, 2000). If Prussian Carp invades lakes, this might pose a problem for recreational fisheries in Alberta, or commercial ventures in larger lakes throughout North America, especially if these ecosystems are already degraded from human activities. Additionally, the synergistic interaction from habitat degradation and Prussian Carp's invasion might expose aquatic ecosystems to other invaders. In Canada there are imminent threats from species such as the Zebra mussel (*Dreissena polymorpha*) that are moving west from the Great Lakes.

The risks Prussian Carp pose to freshwater species in western North America are numerous. Prussian Carp's biological traits and tolerances are attributed to its success in Eurasia, but it is not yet known how this will translate into aquatic ecosystems of western North America. Considering this, it is vital to determine the severity of Prussian Carp's invasion and understand the effects to native fish communities. Determining these key components and relating this to the current understanding of Prussian Carp's invasion in Eurasia, will help fill the present knowledge gaps and help guide management practices for controlling this species in the future.

Chapter 3 : Establishment, spread and impact of Prussian Carp (*Carassius gibelio*), a new invasive species in western North America

Executive summary

Prussian Carp (*Carassius gibelio*) are one of the most devastating invasive species in Eurasia. Recently, Prussian Carp were genetically confirmed in Alberta, Canada. It is likely that the Prussian Carp have gone unnoticed in western North American because they are morphologically similar to the Goldfish (*Carassius auratus*). The arrival of Prussian Carp in western North America poses concerns for many native freshwater species. The objectives of this study were to assess the severity of Prussian Carp's invasion in western North America by 1) mapping Prussian Carp distribution and rate of spread since its initial arrival; 2) analysing the impact of Prussian Carp on native fish species; and 3) identifying environmental parameters that predict Prussian Carp presence. Using kernel density functions, we found that the range of Prussian Carp increased in Alberta, Canada from approximately 500 km² since its arrival (estimated as 2000) to over 20,000 km² in 2014. The rate of spread is increasing at an exponential rate over five year increments (e.g. 1.6, 2.1, and 2.3 times over a 15 year period), suggesting rapid expansion since first detection. The most important habitat variables that best predicted the presence of Prussian Carp were: dense aquatic vegetation, high conductivity, pH, high dissolved oxygen and low flow rates indicating preference for relatively slow, eutrophic streams. Although our results did not indicate that Prussian Carp had a negative effect on native fish species, it is likely due to its recent expansion into these areas and an already depauperate species pool. Given the proximity to the Missouri/Mississippi drainages, agencies throughout North America should be aware of this invasive species and the potential impacts on native biota.

Introduction

Invasive species currently pose one of the highest threats to biodiversity next to climate change and habitat alteration (Aydin *et al.*, 2011). Human encroachment of natural areas and the ease of movement of people and goods has facilitated the introduction of invasive species, intentionally or incidental, around the world (Meador *et al.*, 2003). Intentional introductions arise from species used for recreation, sustenance and aquaculture, biological management, pet trade and ornamental purposes; whereas incidental introductions are a frequent consequence of commerce and tourism (Louda *et al.*, 1997; Ruiz *et al.*, 2000; Sakai *et al.*, 2001; Semmens *et al.*, 2004; Dextrase & Mandrak, 2006). Recent estimates suggest the number of invasive species introduced to the United States, South Africa, Australia, India, United Kingdom and Brazil exceed 120,000 species, with a combined cost of US$ 314 billion annually due to damages (Pimentel *et al.*, 2001). Ultimately, the movement of invasive species can lead to global homogenization of biota and is considered a leading driver for global biological change (Vitousek *et al.*, 1996; Ozulug *et al.*, 2004).

There are four recognized stages of invasion: transportation, introduction, establishment and spread (Williamson & Fitter, 1996). The success of an invasive species in a new environment can depend on many factors such as introduction effort (i.e. propagule pressure), habitat suitability, resource availability and life history attributes of the species (Kolar & Lodge, 2002; Leung & Mandrak, 2007). However, it is estimated that only one percent of species introduced in a new environment will become invasive (Williamson & Fitter, 1996; Hellmann *et al.*, 2008). This is because there are distinct characteristics (or traits) associated with invasive species that increase the likelihood of establishment and proliferation in new habitats. These traits include early sexual maturity, high fecundity, rapid growth, broad diet, asexual reproduction, tolerance to environmental stressors, phenotypic plasticity and attributes that facilitate human-assisted dispersal (Lodge, 1993; Leonardos *et al.*, 2008a; Kirankaya & Ekmekçi, 2013).

Once an invasive species becomes established, it can cause irreversible ecological damage (Sakai *et al.*, 2001; Vitule *et al.*, 2009; Aydin *et al.*, 2011). Invasive species can negatively affect native species through competition for resources or habitat, niche displacement, predation, introduction of foreign pathogens or parasites, and hybridization (Kenward & Holm, 1989; Hänfling *et al.*, 2005; Ruesink, 2005). At a community level, changes in population abundances of different species can shift community structure and disrupt the energy flow within the system, altering trophic dynamics and potentially causing trophic cascades (Simon & Townsend, 2003; Strayer *et al.*, 2006; Gherardi, 2007). These types of alterations can threaten ecosystem resilience and recovery following disturbance events (Olden *et al.*, 2004). Furthermore, invasive species can also interfere with ecosystem processes by altering disturbance regimes, soil properties, or nutrient and water availability (Brooks *et al.*, 2004; Ruesink, 2005; Strayer *et al.*, 2006). Such impacts on biotic and abiotic habitat factors may ultimately lead to population decline or extirpations among native species (Ricciardi *et al.*, 1998).

Aquatic ecosystems, in general, experience a higher rate of establishment of invasive species than terrestrial ecosystems (Williamson & Fitter, 1996). For example, of the 1,424 intentional introductions of 200 different species into aquatic systems around the world since 1850, 64% have become established, and subsequently 22% of the established species became invasive (Ruesink, 2005). The higher probability of establishment of aquatic invasive species is thought to be aided by a combination of good inherent dispersal ability by aquatic organisms and by many freshwater communities not being replete with species that fill the ecological niche space (Cornell & Lawton, 1992; Ricciardi & MacIsaac, 2000). Because of the high dispersal ability of aquatic species, eradication and controlling invasive species is often problematic because there are limited ways of removal without affecting native species as a result (Gherardi, 2007). The estimated economic losses associated with invasive fish in the United States alone is US$5.4 billion annually (Pimentel *et al.*, 2005).

Recently, Prussian Carp (*Carassius gibelio,* Bloch 1782), one of the most harmful invasive fish in Eurasia (Kalous *et al.*, 2004), has been found in western North America (Elgin *et al.*, 2014). This species was first documented in south-central Alberta, Canada in the year 2000 (ESRD, unpublished data). Prussian Carp are native to northern China, but through intentional or incidental introduction, its range extends into Europe from the Baltic Sea to the Mediterranean (Vetemaa *et al.*, 2005; Tarkan *et al.*, 2014). Prussian Carp are morphologically similar to another common *Carassius* species, the Goldfish (*Carassius auratus*), often leading to misidentification and delayed detection in newly invaded systems, which may have been the case in North America (Aydin *et al.*, 2011). In western Canada, Prussian Carp have unequivocally been identified through genetic analysis in 2014 (Elgin *et al.*, 2014).

Potential concerns associated with Prussian Carp in North America are numerous. Prussian Carp thrive in slow moving or stagnant water, and are known to aggressively colonize new habitats to become the most the dominant species (Sarı *et al.*, 2008). They possess a number of the qualities identified in highly invasive species, including the ability to tolerate extreme environmental conditions such as low oxygen, eutrophication and high turbidity; and they have a broad, omnivorous diet consisting of macrophytes, detritus and invertebrates (Balik *et al.*, 2003). Their environmental plasticity is high (Gaygusuz *et al.*, 2007); and lastly, they are capable of reproducing sexually through gynogenesis (Zhou *et al.*, 2003; Tsoumani *et al.*, 2006). A major concern for displacement of native species is that Prussian Carp can degrade water and habitat quality by disturbing sediment during foraging (Crivelli, 1995) and several studies have observed declines in native fish species post-introduction and establishment of Prussian Carp (Kalous *et al.*, 2004; Gaygusuz *et al.*, 2007; Tarkan *et al.*, 2012a).

In this study we contribute a population survey of Prussian Carp and a threat assessment for native fish species in western North America. We assess 1) the establishment of Prussian Carp in western North America, 2) the spread of Prussian Carp since its arrival in western North America, 3) environmental predictors of Prussian Carp presence, and 4) impacts to native fish community assemblages after Prussian Carp establishment. Addressing these objectives will help to fill key gaps in knowledge regarding the establishment of Prussian Carp in North America and help managers to set restoration and conservation goals.

Methods

Establishment of Prussian Carp

We conducted field surveys on 12 streams within the Red Deer watershed (51° 40.407' N, 113° 18.707' W), approximately 130 km north-east of Calgary, Alberta, the epi-centre of Prussian Carp invasion (Fig. 2). This area is situated at the intersection of four different ecoregions: Northern Fescue, Foothill Fescue, Central Parkland and Mixed Grassland (Natural Regions Committee, 2006). The climate is continental with approximately 420mm annual precipitation and 2°C mean annual temperature. The topography for the region is relatively flat with sections of undulating hills, and streams are slow moving, low gradient and sinuous. The dominant anthropogenic activities are agriculture, which can occupy over 85 percent of the land base in some areas, followed by urbanization and industrial activities (Dodds et al., 2004; Natural Regions Committee, 2006).

Site selection for sampling was based on areas where the species was not yet known to be established as of 2005 (Stevens *et al.*, 2006), but thought to occur as of 2014 (J. Cooper, AESRD pers. comm.). Field surveys covered an area of approximately 4,700 km^2 in the Red Deer River watershed, including the following tributaries: Ghostpine Creek, Three Hills Creek, Kneehills Creek, Lonepine Creek, Rosebud River, Carstairs Creek, Crossfield Creek, West Michichi Creek, Michichi Creek, and three unnamed streams (Fig. 2). Each site consisted of a 300m wadeable stream or river section, and was sampled for the fish community, water quality, substrate type and amount of aquatic vegetation (Alberta Fisheries Management Branch, 2013).

Electrofishing was conducted using a standardized single-pass electrofishing procedure in an upstream direction with a Smith-Root LR-24 backpack electrofisher for an average of 1734 seconds (502-3173 seconds) (Alberta Fisheries Management Branch, 2013). Targeted survey time was 1500 seconds to ensure adequate sampling of fish community (Poos *et al.*, 2009).Variations in sampling effort were due to differences in site characteristic (i.e. stream width).

At each sample site, all species caught were enumerated and a sub-sample of native species (≤ 20 specimens) and all Prussian Carp were measured for total length, weight and assessed for overall condition (i.e. Fulton's condition factor). All species caught were standardized to catch per unit effort (CPUE) per 100 seconds (hereafter referred to as abundance). After fish collection, habitat data was collected at each site. Stream width and water depth were measured at three points across the river and then averaged for each site. Water quality parameters were measured midway across the stream in a location representative of the site. Dissolved oxygen ($\pm$ 0.2 $mg \cdot L^{-1}$), conductivity ($\pm$ -0.01$mS \cdot cm^{-1}$) and pH were recorded using a multimeter (YSI, Yellow Springs, Ohio). Turbidity samples were collected using a portable turbidity meter (LaMotte 2020we) for turbidity (± 50 nephelometric turbidity units, NTU) in the upper 30 cm of the water column and stream velocity was measured at mid water depth. Percent composition of aquatic vegetation, riparian vegetation, and stream substrate were estimated through visual assessment of the entire 300-meter sampling site (Alberta Fisheries Management Branch, 2013).

To determine Prussian Carp condition and demographic structure in 2014, we calculated a length frequency distribution, length-weight regression and an indicator of condition (i.e. Fulton's condition factor) using the R programming environment (R Development Core Team, 2014). Here, condition factor (K) is defined as:

$$K = 100\left(\frac{W}{L^3}\right)$$

Where, W is the weight (grams) and L is the length (cm) of an individual fish (Heincke, 1908).

Spread of Prussian Carp

To assess the spread of Prussian Carp since establishment, we conducted an analysis of all available census data sources in river and lake systems throughout the provinces of Alberta and Saskatchewan in Canada from 1999-2014 (FWMIS, 2015; D. Watkinson, Fisheries and Oceans Canada, pers. comm.). Non-confirmed localities were not included in our assessment. To determine rate of spread and the highest density of Prussian Carp in Alberta, we evaluated spatial plots in 4-year intervals using a kernel density analysis and percent volume contours from the Kernel Density tool in ArcGIS and Isopleth tool of the Geospatial Modeling Environment (Beyer, 2012) for ArcGIS, respectively. Kernel densities are useful for calculating a species home range based on the likelihood that a species can be found in a specific region (Fortin *et al.*, 2005). They are calculated by fitting a kernel (i.e. a weighted curve) over a point with a specific radius (Worton, 1989). Here, we set the search radius to 25 km^2 to summarize regional scale changes in their range throughout Alberta. Each kernel is additive, therefore, areas with higher point densities will have higher kernel densities and be represented as darker regions of the map. Likewise, percent volume contours help estimate the potential core (50%) and range extent (95%) at each temporal stage of invasion.

Environmental Predictors of Prussian Carp presence

We assessed the associations of Prussian Carp abundance with 14 environmental and habitat variables (Table 1) for the 2014 surveys (n=41). Habitat features such as aquatic vegetation (i.e. % cover), substrate (i.e. %clay, % silt, % sand, % gravel), water velocity and geomorphological characteristics (i.e. stream length, width and depth) have been shown to relate to micro-habitat features (Vanote *et al.*, 1980; Poos *et al.*, 2008). Water quality indicators such as temperature, dissolved oxygen, pH, and turbidity influence the abundance and distribution of stream biota (Richter *et al.*, 1997). Finally, electrical conductivity is explicitly linked to dissolved ions in the water and acts a proxy for stream productivity (Alberta Fisheries Management Branch, 2013).

To assess variable importance we used Spearman's rank correlation coefficients for non-parametric data, implemented with the *rcorr* function of the *Hmisc* package (Harrell, 2015) for the R programming environment. Secondly, we used the ensemble classifier *Random Forest* to assess which variables best predict Prussian Carp abundance using a Variable Importance statistic (Breiman, 2001; Liaw & Wiener, 2002). The *Random Forest* approach was chosen because, like Spearman's rank correlations, it is appropriate for non-parametric data and non-linear relationships. In addition, it takes interactions among environmental predictor variables into account by associating high or low values in the response variable with combinations of different predictor variable values (Breiman, 2001; Hastie *et al.*, 2009). For example, high abundance of a species may be associated with high values in predictor X and intermediate values in predictor Y, but not with any other variable combinations.

Impact of Prussian Carp on native fish communities

We assessed changes to fish assemblages in areas where Prussian Carp were present. In total, six native species were detected in these areas, including: Fathead Minnow (*Pimephales promelas*), White Sucker (*Catostomus commersoni*), Lake Chub (*Couesius plumbeus*), Brook Stickleback (*Culaea inconstans*), Longnose Dace (*Rhinichthys cataractae*), and Longnose Sucker (*Catostomus catostomus*). The sampling effort for each species was standardized to catch per unit effort (CPUE; i.e. abundance of each species per 100 electrofishing seconds at each site). Sample sites were separated into three groups based using natural breaks in Prussian Carp abundance in our survey: 1) no Prussian Carp (n = 13 sites), 2) low Prussian Carp (i.e. 0.05 - 0.10 CPUE/100 seconds; n = 20 sites), and 3) high Prussian Carp (i.e. 6 – 8 CPUE/100 seconds; n = 8 sites). We used Non-Metric Multidimensional Scaling (NMDS) analysis to investigate the differences between Prussian Carp abundance groups using the *Ecodist* package (Goslee & Urban, 2007) for the R programming environment. The NMDS was selected because it is a non-parametric technique which avoids assumption of linear relationships between variables and minimizes distortion when graphically displaying the distances between samples (Kruskal, 1964; McCune et al., 2002).The NMDS ordination was carried out based on the Bray-Curtis multivariate distance metric (McCune *et al.*, 2002; & Coe, 2005). To visually assess the variance in fish communities within and among groups of sites, we plotted the first two NMDS dimensions. Permutational MANOVA was used to test for significant differences within and among groups because this method does not make assumptions for normality of the data

(Anderson, 2005). The permutational MANOVA was conducted using the *adonis* function in the *vegan* package (Oksanen *et al.* 2015) for the R programming environment.

Results

Establishment of Prussian Carp

Prussian Carp were found in 68% of the sites of our 2014 survey approximately 188 km of stream and river**.** In total we captured 2,587 Prussian Carp, including 1,492 individuals from a single site. From a sub-sample of 625 Prussian Carp specimens, average total length was 78 mm (29-196 mm) and average weight was 8.8 g (0.25 – 150 g). In most cases, multi-years classes were present at sample sites, suggesting successful reproduction and self-sustaining populations of Prussian Carp (Fig. 3). A majority of fish were between 40 mm and 120 mm, with the highest frequency at 80 mm (Fig.3, Fig. 4); most likely representing 0-2 year classes (Fig.3). The largest individual caught was 196 mm, presumably representing 3+ age class. Fulton's condition factor was 1.36 (± 0.309) for Prussian Carp specimens caught in 2014, indicating Prussian Carp are in good condition.

Spread of Prussian Carp

Spatial analysis of spread by kernel density estimates suggest that Prussian Carp as become well established in Alberta, Canada. Since the year 2000, Prussian Carp have increased from about 500 km^2 spatial extent to over 20,000 km^2 in 2014 (Fig. 2). We found that the range of Prussian Carp is increasing at an exponential rate over five year increments (e.g. 1.6, 2.1, and 2.3 times over a 15 year period) in Alberta, Canada, suggesting rapid expansion since first detection. The highest density of Prussian Carp occurred in the north-western region of the study area, with a core distribution of about 5000 km^2 (Fig. 2e). Four tributaries sampled in 2014 that yielded the high numbers of Prussian Carp including Kneehills Creek, Michichi Creek and two unnamed creeks, potentially indicating prolonged time since establishment or highly suitable habitat. Finally, we found Prussian Carp in both artificial and natural waterways, mainly in small tributaries and rarely in larger river systems (Fig. 2).

Environmental Predictors of Prussian Carp presence

Prussian Carp were found across a large range of environmental and habitat conditions. To graphically describe the relationship between Prussian Carp and habitat and environmental variables, scatterplots were created with Spearman's rank-order correlation coefficients and tested for significance for variables that displayed a positive or negative correlation with Prussian Carp abundance (Fig.5). Here, we found that Prussian Carp abundance was only significantly correlated with aquatic vegetation (p=0.01, Fig. 5).

The Random Forest variable importance model, taking into account potential interactions among variables, yielded similar result as the spearman coefficients, where the most important variables in predicting Prussian Carp's presence included aquatic vegetation, conductivity, and pH (Fig. 6).

Impact of Prussian Carp on native fish communities

There was no apparent impact of Prussian Carp on fish community composition based on the ordination of sites grouped by no, low, or high Prussian Carp abundance (Fig. 7, Fig. 8). Instead, sites with high Prussian Carp abundance generally had high abundance in all other species as well, suggesting that other environmental factors influence abundance of all species irrespective of Prussian Carp presence (Fig. 7, Fig. 8). The lack of species vectors in Fig. 8 that are opposite in direction to Prussian Carp abundance indicates no apparent negative effect of one species on another (or the occupancy of different niche space). Most species had a low to moderate positive association with Prussian Carp. Permutational MANOVA demonstrated no significant differences among no, low or high Prussian Carp abundance (p=0.416, df=2).

Discussion

This study documents the establishment and relatively rapid spread of Prussian Carp in Alberta, Canada over the last 15 years. This invasion is, in part, attributed to habitat preferences for slow moving or stagnant aquatic habitats, as well as habitats that are marginal or disturbed (Slavík & Bartoš, 2004; Vetemaa *et al.*, 2005; Tsoumani *et al.*, 2006; Leonardos *et al.*, 2008a), which was also confirmed by our analysis of habitat factors. In Europe and western Asia, Prussian Carp were predominantly found in lakes, streams with low water velocities and estuaries and less frequently in fast flowing main channels (Slavík & Bartoš, 2004; Tsoumani *et al.*, 2006; Özcan, 2007). In fact, increasing stream gradient was observed to be a barrier to movement (Slavík & Bartoš, 2004). Similarly, Prussian Carp were mainly found in small tributaries with low water velocities and rarely found in larger river systems in this study.

The spread of Prussian Carp in Alberta, Canada is likely further enhanced by the utilization of artificial waterways and human facilitated movement. For instance, during our analysis of prior survey data, we identified what appears to be at least three separate introduction events, to locations where Prussian Carp are found beyond known barriers, requiring human assistance. Many of these locations are artificial habitats such as ponds, reservoirs and irrigation canals. Prussian Carp's ability to thrive in artificial habitats is not uncommon and several studies have shown their high affinity for reservoirs, ponds and deep, mesotrophic lakes with minimal vegetation, that deviate from typical observed habitat preferences (Ozulug *et al.*, 2004; Aydin *et al.*, 2011). It is possible that an extensive network of irrigation canals in the study area may have aided in the spread of Prussian Carp throughout this region.

There is a high likelihood that Prussian Carp will spread beyond Alberta, Canada and into other areas in western North America. Given both the proximity and the large network of canals within Alberta, Prussian Carp have the potential to move through the Milk River basin, which connects to the Missouri River system, and further south into the Mississippi and throughout the continental United States. If Prussian Carp were to reach the Mississippi drainages, it is likely that they would flourish. Prussian Carp have been listed as a 'high risk' invasive species based on its history of invasiveness in Eurasia, biological characteristics, and climatic compatibility with the majority of the continental United States, particularly in the mid-west and Great Lakes region (U.S. Fish and Wildlife Service, 2012). In fact, during our investigation we identified a single Prussian Carp found near Swift Current, Saskatchewan (D. Watkinson, Fisheries and Oceans Canada), the first confirmed sighting outside of Alberta, Canada.

While not all invasive species have negative impacts on native species communities, Prussian Carp exhibits many characteristics of a prolific invasive species that suggest its introduction, establishment and spread in western North America will be of concern (Kolar & Lodge, 2002; Sarı *et al.*, 2008). Of particular importance is Prussian Carp's ability to reproduce asexually through gynogenesis. This type of reproduction is most prevalent in recently colonized areas and is one of the main factors contributing to Prussian Carp's success in new environments (Kalous *et al.*, 2004; Aydin *et al.*, 2011). Unlike sexual reproduction, gynogenetic reproduction utilizes the sperm of interspecific species, namely other minnows (family *Cyprinidae*, hereafter cyprinds), to activate egg development but contributes no genetic material (Gui & Zhou, 2010). In Alberta, there is evidence from one site that suggests Prussian Carp are reproducing through gynogenesis. Population estimates from the Rosebud River sub-watershed, Alberta, found the sex ratio of self-sustaining Prussian Carp populations to favour females (62% females, 23% males and 15% undetermined), and the majority of juveniles were reaching sexual maturity within the first year (Henderson, 2012).

In Europe and western Asia, declines in native cyprinids have been linked to reproductive interference from Prussian Carp (Tarkan *et al.*, 2012a). Cyprinids, which are the main species targeted during gynogenesis, are the most widespread and diverse family of fish in North America (Joynt & Sullivan, 2003). Their broad distribution makes them highly susceptible to reproductive interference and also provides ample opportunities for Prussian Carp to expand its range by exploiting the sperm of local species. Additionally, native cyprinids may experience declines from competition for resources and habitat as Prussian Carp becomes more abundant. A cyprinids role in any ecosystem will vary depending on the system and species, but generally, most cyprinids occupy lower trophic levels and feed on invertebrates, macrophytes, detritus and plankton, with only a few larger species in North America consuming other fishes (Buth *et al.*, 1991). Indeed, Prussian Carp's diet and habitat preferences overlap with many species in North America and the likelihood of future competition is high (Coker *et al.*, 2001). Competition between Prussian Carp and local cyprinids could lead to declines or extirpations, resulting in unintended tropic restructuring or cascading (Carpenter *et al.*, 1985). Although our results did not indicate that Prussian Carp are currently having a negative effect on native species (Fig. 8); this could be due to the relatively recent establishment in most parts of the study area. For example, there is often a lag-affect where invasive species remain at low levels in a new environment, then expand rapidly (Mooney & Cleland, 2001). This is likely the case in Alberta because Prussian Carp was not a dominant species on the majority of our sampling sites, while in European studies of Prussian Carp, it is usually the most abundant species in these communities once fully established (Balik *et al.*, 2003; Özcan, 2007; Sarı *et al.*, 2008). Additionally, prairie fish are inherently hardy in this region due to the harsh environmental conditions and unstable hydraulic regimes. Further, shifts in fish community from anthropogenic activities (i.e.

agriculture) have reduced the historical pool of species to the most tolerant species capable of withstanding the additional stress (Matthews, 1988; Rabeni, 1996; Dodds et al., 2004). While Prussian Carp populations remain low, it is likely native fish are able to absorb additional stress exerted from Prussian Carp in these aquatic systems.

Local species may experience indirect effects of Prussian Carp's establishment and spread in western North America. Invasive species can act as ecosystem engineers, facilitating habitat degradation that threatens native species and enhances the likelihood of future invasions (i.e. invasional meltdown hypothesis; (Ricciardi, 2001)). Although there are no studies that specifically link Prussian Carp to subsequent invasions, habitat degradation from Prussian Carp have been reported in Europe followed by a decline in native species (Navodaru *et al.*, 2002; Balik *et al.*, 2003). Crivelli (1995), for instance, observed an increase in turbidity that corresponded with the invasion of Prussian Carp in Lake Mikri Prespa, Greece, as a product of foraging behaviour. Increases in turbidity can negatively affect native fish species by decreasing foraging success by limiting visibility, reducing available spawning habitat from siltation and directly interfering with gill function (Rabeni & Smale, 1995; Utne-Palm, 2002; Chapman *et al.*, 2014). Further, Prussian Carp's foraging strategy not only increases turbidity, it can also release nutrients deposited in benthic sediment into the water column (Crivelli, 1995). Nutrient enrichment can have unintended ecological consequences including shifts in trophic structure (i.e. the bottom-up affect) by elevating levels of primary productivity (Weber & Brown, 2009; Chapman *et al.*, 2014). Increases in primary productivity can be beneficial in some systems or can exacerbate eutrophication in others, the resulting habitat may be inhospitable for native fish species (Carpenter, 2005). Thus, this is a relatively novel disturbance for native ecosystems, where ecosystem engineering by Prussian Carp may alter the state of the wider ecosystem with the potential to create a more degraded, less resilient system that is more susceptible to natural and other novel disturbances.

Not only can Prussian Carp cause habitat degradation, they are recognized for their ability to thrive in habitat unsuitable for most other species (i.e. hypoxia, environmental pollution, moderate salinity, turbidity and high levels eutrophication) (Vetemaa *et al.*, 2005; Leonardos *et al.*, 2008b; Liasko *et al.*, 2011). These specific tolerances allow Prussian Carp to persist and outcompete native species, particularly those sensitive to disturbance. Such environmental extremes were encountered during our field survey, when 1,492 Prussian Carp were found surviving in a small pool with only 2% dissolved oxygen. Generally, Prussian Carp were found in a wide range of environmental and habitat conditions in our field survey, however, the highest abundances were in streams where conductivity and aquatic vegetation was high (Fig. 5 and 6). Dense aquatic vegetation can be an indication of eutrophication, a product of anthropogenic activities such as agriculture (Chambers *et al.*, 2008). Prussian Carp are known to flourish in eutrophic environments and tend to colonize aquatic systems as the level of eutrophication increases (Leonardos *et al.*, 2008b; Paulovits *et al.*, 2014). In many parts of western North America, aquatic habitat integrity is often compromised due to anthropogenic pressures from agriculture, industrial and other human activities (Dodds *et al.*, 2004; McCleary & Hassan, 2008). Although, many of these fish species are relatively hardy (Matthews, 1988), the persistence and proliferation of Prussian Carp throughout North American waterways could be an additional stress on an already strained system.

The establishment and rapid spread of Prussian Carp in the last 15 years that we documented in this study should serve as an alert for fisheries managers across North America. Prussian Carp are recognized as one of the most harmful invasive fish species in Eurasia (Kalous *et al.*, 2004). Their highly prolific reproductive strategy and environmental plasticity allows them to thrive in a variety of habitats, posing a significant threat for North American aquatic systems. In all likelihood, the distribution of Prussian Carp will continue to expand. Extensive irrigation systems and natural drainages provide ample opportunities for range expansion. As there are no successful management strategies available, it is pertinent that fisheries agencies throughout western North America become aware of this species as monitoring, detection and subsequent control may be the only effective strategy for mitigating impacts.

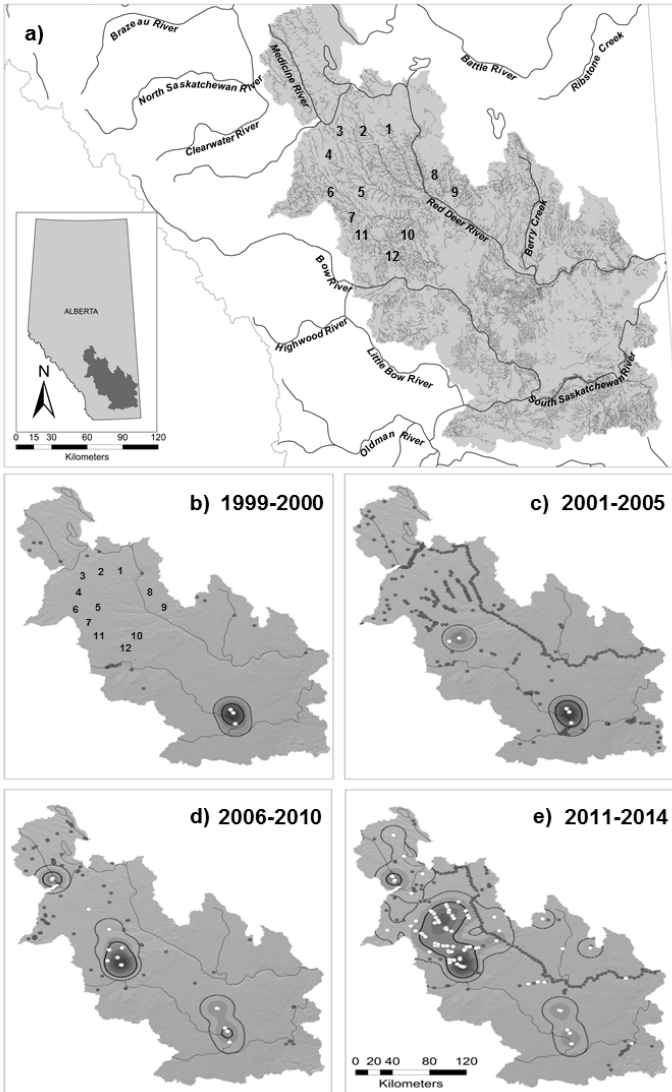

Figure 2 - Five panel map showing study area (a) with fine scale (grey) and major rivers (black) in Southern Alberta. Tributaries sampled include: Ghostpine Creek[1], Three Hills Creek[2], Kneehills Creek[3], Lonepine Creek[4], Rosebud River[5], Carstairs Creek[6], Crossfield Creek[7], West Michichi Creek[8], Michichi Creek[9], and three unnamed streams[10,11,12]. Shown inset is the spread of Prussian Carp (*Carassius gibelio*) in the Alberta, Canada between 2000-2014 (b,c,d,e). Shown are core (50% kernel densities; solid lines) and total distribution (95% kernel densities; dashed lines) for all known Prussian Carp occurrences (open circles). Sites absent of Prussian Carp are shown in closed circles.

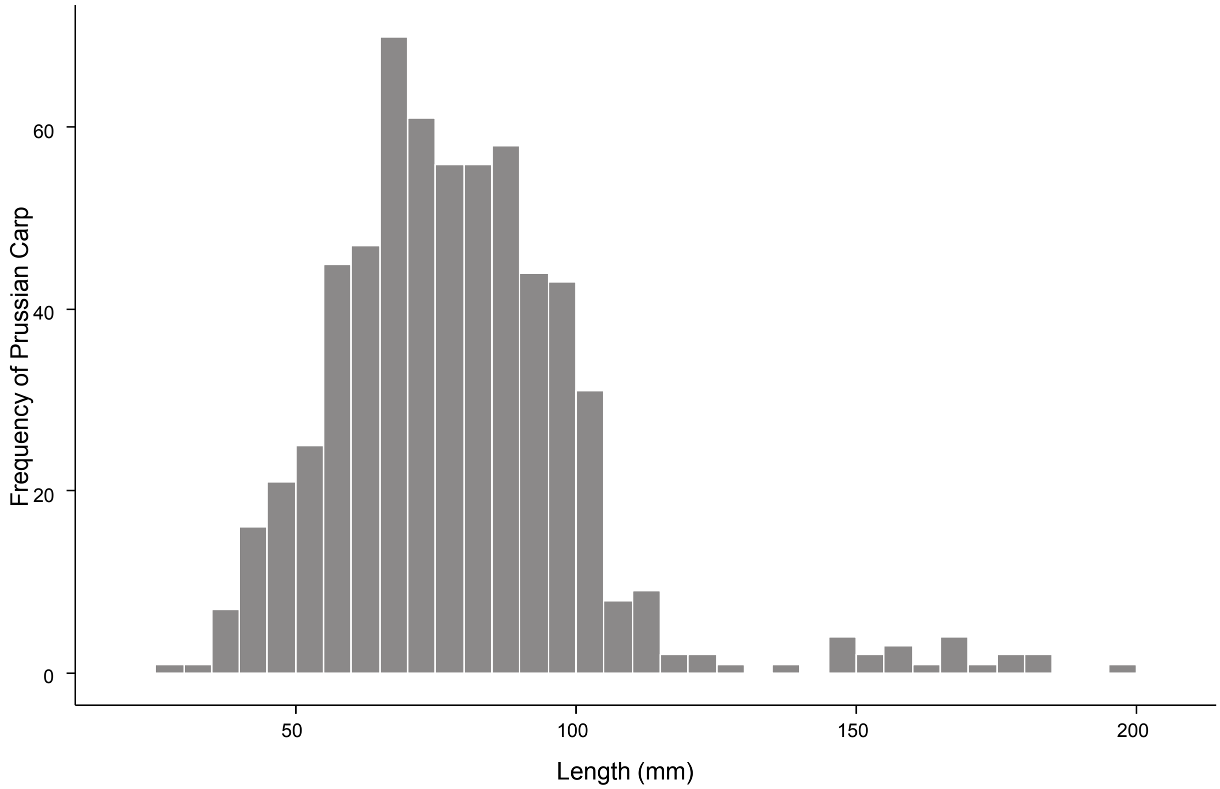

Figure 3 - Length Frequency distribution of Prussian Carp (n=625) collected from sampling in 2014.

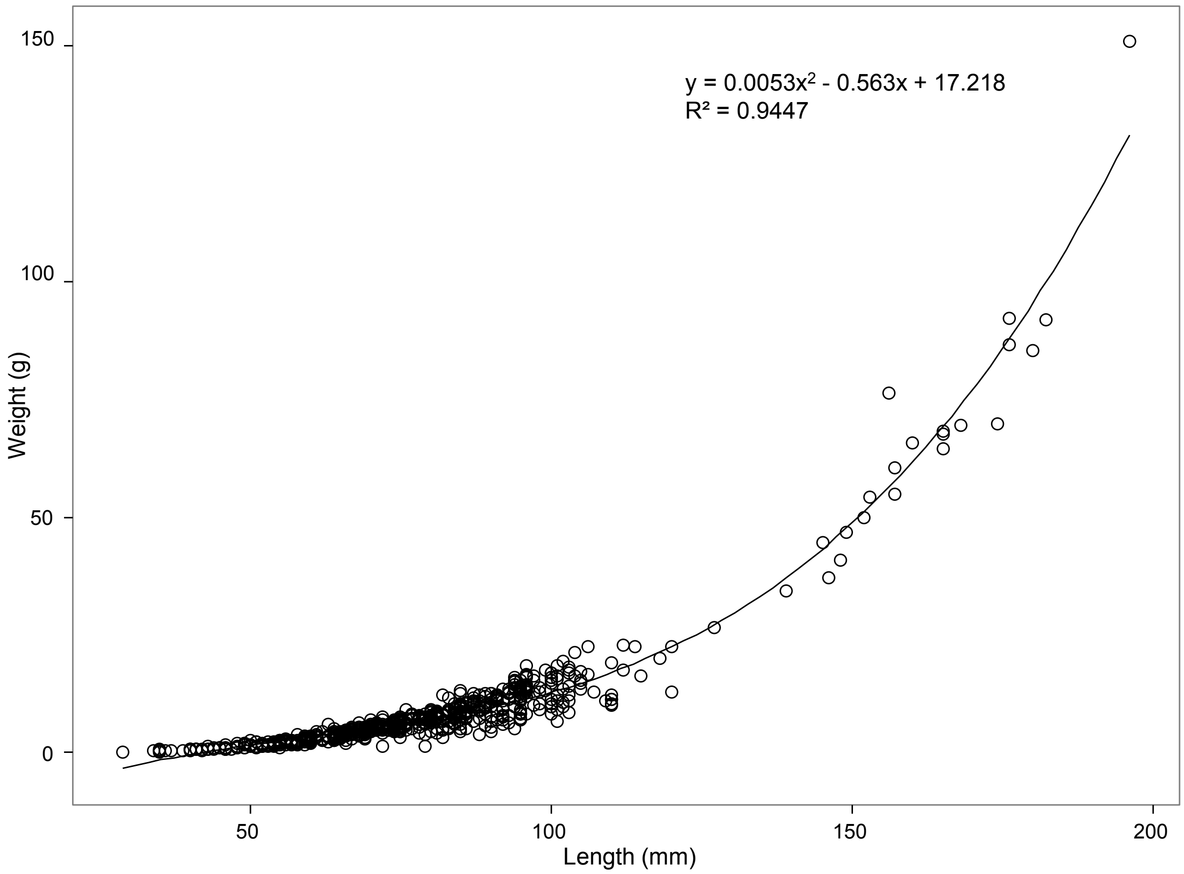

Figure 4 - Length (total length, mm)-weight regression for Prussian Carp from sampling in 2014 (n=625)

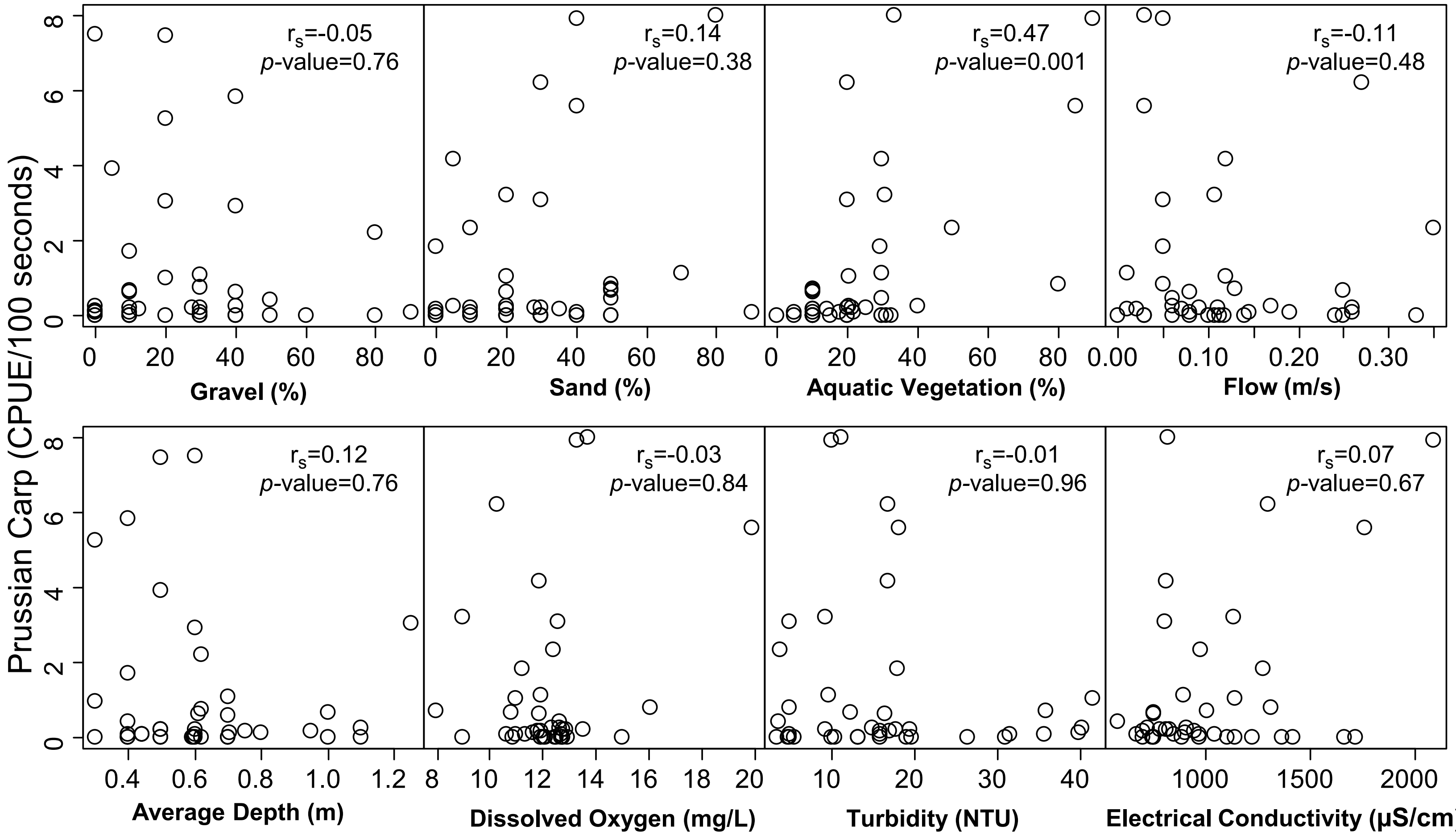

Figure 5 - Relationship between Prussian Carp abundance and eight environmental and habitat variables collected in 2014 using Spearman coefficients (r_s) and p-values.

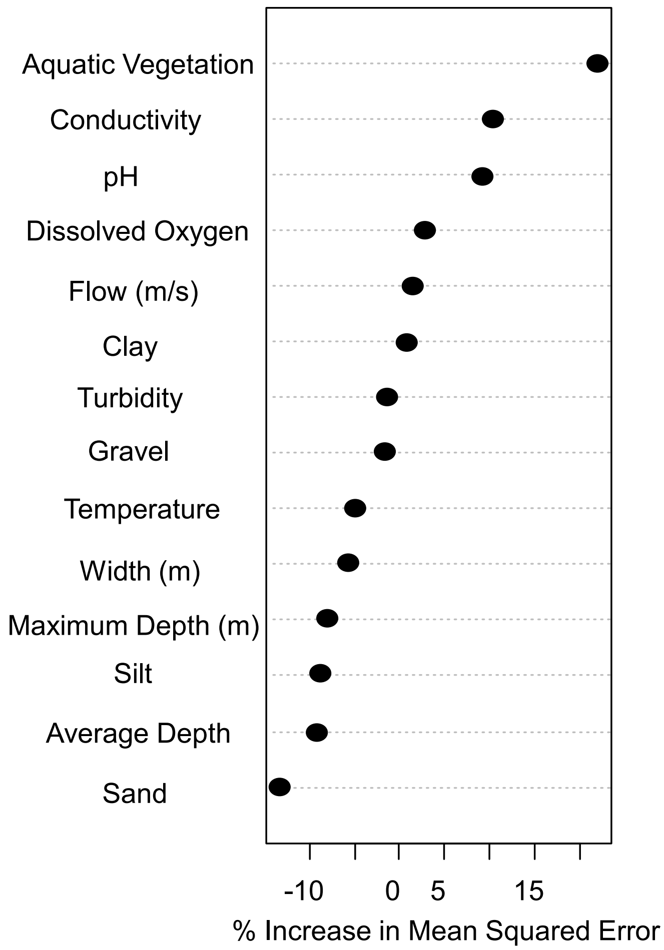

Figure 6 - Random Forests' variable importance plot showing the increase in percent mean squared error (%MSE) for all habitat and environmental variables collected during sampling in 2014, where higher %MSE indicates greater variable importance.

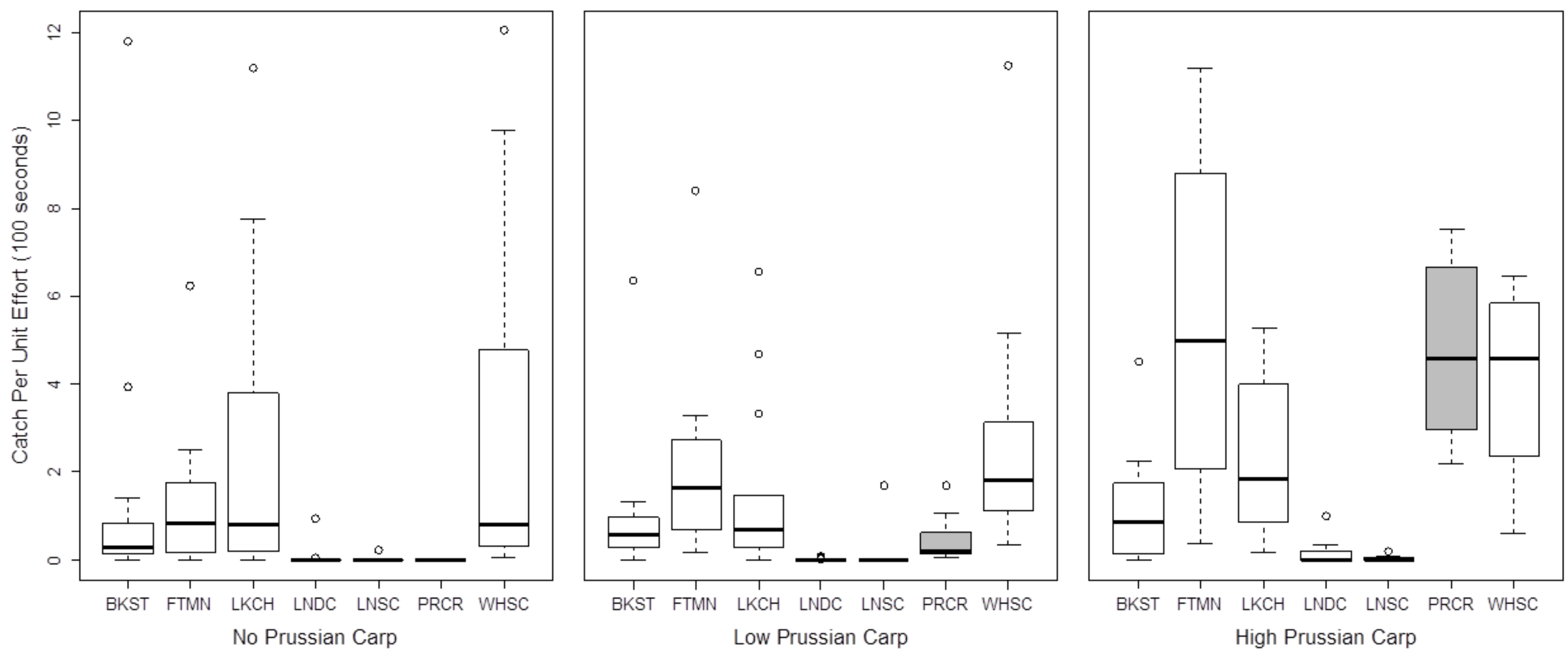

Figure 7 - Difference in species composition and abundance between sites with no, low and high Prussian Carp (grey fill) from sampling in 2014. Black bar indicates median and error bars indicate the maximum and minimum values for each species. Species present include Brook Stickleback (BKST), Fathead Minnow (FTMN), Lake Chub (LKCH), Longnose Dace (LNDC), Longnose Sucker (LNSC), Prussian Carp (PRCR) and White Sucker (WHSC).

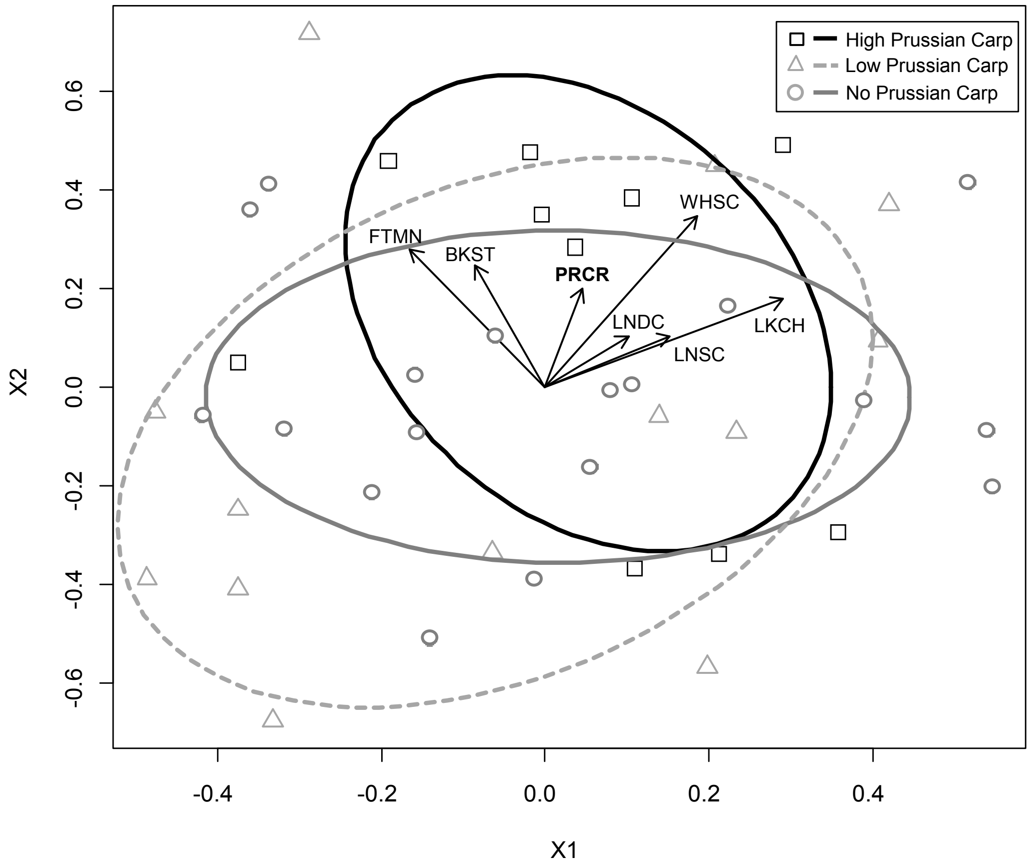

Figure 8 - Nonmetric multidimensional scaling ordination technique using Bray Curtis dissimilarity for sites with no (grey circles), low (grey triangles) and high (black squares) Prussian Carp from 2014 displayed in 2 dimensions (stress: 0.207). Each ellipse corresponds to associated groups for Prussian Carp abundance and vectors indicate the strength of relationship between species and sites captured in 2014. Species present include Fathead Minnow (FTMN), White Sucker (WHSC), Lake Chub (LKCH), Brook Stickleback (BKST), Longnose Dace (LNDC), Prussian Carp (PRCR) and Longnose Sucker (LNSC).

Table 1 - Averages and range values for all environmental and habitat variables collected in 2014

Variable	**Mean**	**Min**	**Max**
Temperature (°C)	4.6	0.8	12.2
pH	9.1	8.2	9.46
Length (m)	288	49	300
Width (m)	3.6	0.4	10
Average Depth (m)	0.6	0.3	1.25
Maximum Depth (m)	1.0	0.5	1.5
Flow (m/s)	0.1	0	0.35
Clay (%)	4.8	0	100
Silt (%)	40.2	0	100
Sand (%)	29.0	0	90
Gravel (%)	25.7	0	90
Aquatic Vegetation (%)	24.8	0	90
Dissolved Oxygen (mg/L)	12.2	8.0	19.9
Turbidity (NTU)	16.2	3.3	41.5
Electrical Conductivity (μS/cm)	1018	582	2089

Chapter 4 : Management and conclusions

Overview of available management techniques

The first step in management of an invasive species is detection. Aquatic invasive species are inherently difficult to detect and manage because they are concealed below the water's surface (Jerde *et al.*, 2011). Conventional sampling methods, such as seining and electrofishing, have been traditionally used to detect invading species, but both of these techniques have low capture efficiency unless population abundances are high (Magnuson *et al.*, 1994). More recent technological advances in detection include the use of environmental DNA (eDNA). This process works by extracting fish DNA from the water column to determine whether a species is present or not (Jerde *et al.*, 2011). This technology can be readily utilized by agencies as a simple, non-invasive way to monitor a species invasion front (i.e. the extent of their distribution), even when populations persist at low levels (Jerde *et al.*, 2013).

Once a species has been detected, there are only a few options available for successful eradication or control of aquatic invasive species. These methodologies come in several forms with varying degrees of effectiveness. The four main strategies implemented by managers include: physical barriers to movement, non-physical behavioural response barriers, chemical control and biological control (Bourne *et al.*, 2011). Physical barriers typically constitute any obstacle that will inhibit a fish's ability to swim, jump, leap or climb upstream such as dams, weirs, gates and fences (Bourne *et al.*, 2011). Physical barriers can be effective at preventing fish passage but they are often expensive to build and maintain and also restrict passage of native species (Hunn & Youngs, 1980). Non-physical behavioural response barriers work by targeting certain morphological and physiological features on a fish's body (e.g. inner ear, lateral line or swimming ability) evoking an avoidance response to deter passage (Noatch & Suski, 2012).

These barriers include electric barriers, strobe lights, sound barriers, velocity barriers and bubble walls (Noatch & Suski, 2012). The electrical barrier is perhaps the most effective, but most of these methodologies are not useful unless combined with other deterrent techniques (Reynolds *et al.*, 1996). Chemical application of piscicide, such as Rotenone, is the most lethal technique and likely most effective. However, there are some caveats of using piscicide including the requirement for shallow lakes (<10 meter) or very slow flowing water, not to mention the undesired killing of non-target species (Rowe, 2001). Furthermore, biological control uses biological agents such as predators, pathogens and parasites to control populations of invasive species (Thresher *et al.*, 2014). Biological control can also include genetic or chemo-sterilization to reduce egg viability and skew sex ratios (Bergstedt *et al.*, 2003). The latter method can be highly effective at controlling populations, especially when combined with other tactics, and does not negatively affect native species (Bergstedt *et al.*, 2003).

Management of Prussian Carp

Now that our research has confirmed Prussian Carp's invasion in western North America, consideration on management and employment of these techniques may be necessary to prevent further spread. In reality, eradication of Prussian Carp is virtually impossible, but there may be some strategies to reduce population numbers and limit the effects on the local ecology. Of the feasible management options, electric barriers would be useful for targeting streams or canals systems with high densities of Prussian Carp, especially if these systems are source populations for the catchment. However, the ecological cost to this method would be the restriction of native species movement. Similarly, physical barriers such as gates, fencing or weirs may be useful to prevent movement of Prussian Carp as they does not do well at overcoming barriers, but this method would also impede movement of native species (Slavík & Bartoš, 2004). As indicated, the most effective way to exterminate Prussian Carp would be applying a piscicide. Although piscicide is not effective in fast flowing water, the slow flowing reaches of Albertan streams may be satisfactory (Lintermans & Raadik, 2001). Timing can also play an important role in piscicide application. For instance, Prussian Carp could be targeted during spawning or in over wintering areas to increase effectiveness, but there is almost no way to do this without sacrificing native species (Rowe, 2001). Even if this management technique was employed, there are dose-response considerations. Prussian Carp have a high resistance to intoxication and it has been demonstrated by Ling (2003) that *Carassius* species need one of the highest doses of piscicide for the longest duration. An application of this magnitude on prairie streams would likely transport the piscicide far outside the target area, resulting in increased fish mortality. Lastly, it appears that Prussian Carp are reproducing through gynogenesis in Alberta; therefore, there may be an opportunity to use the cyHV-2 cyprinid herpes virus that caused the mass mortality of triploid females in the Czech Republic as a biological control (Daněk *et al.*, 2012).

While the physical containment or removal of Prussian Carp may be one component of management, the successful control of this species will need to involve the integration of the scientific and socio-economic aspects as well (Aquatic Biosecurity & Risk Management Unit, 2010). Firstly, Prussian Carp control should be a part of a larger watershed management plan because if stream health is compromised from external factors, it is unlikely that removing Prussian Carp will improve overall stream health. For this reason, it is imperative to investigate the temporal changes in native fish communities throughout the prairie regions of western North America by conducting comprehensive stream surveys. This is necessary to elucidate the ecological impact of Prussian Carp to native species, target high risk areas, as well as distinguish any confounding factors (Vitule et al., 2009). Government agencies can focus on prevention by setting up stricter regulations for import and increasing surveillance between provincial and national borders. The extraction of eDNA can be a very useful tool to track the dispersal of Prussian Carp and identify the invasion front (Jerde *et al.*, 2013). Another form of prevention could also focus on stream restoration (or prevention of further degradation) to rehabilitate fish communities and increase ecosystem resiliency (Aquatic Biosecurity & Risk Management Unit, 2010). For example, researchers claim that the decline of large predatory species from over fishing contributed to the spread and dominance of Prussian Carp in Eurasia (Vetemaa *et al.*, 2005). In the context of Alberta and the greater prairie region, it may be beneficial to ensure that populations of large predatory fish are healthy in lakes and rivers, particularly in regions near the invasion epi-center to help control the spread. Any management plan for Prussian Carp should involve the integration of different levels of government, local organizations and the public (Aquatic Biosecurity & Risk Management Unit, 2010). Since resources, which include funding and personnel are often one of the largest impediments facing natural resource managers, public awareness through education and participation could become an asset for managing Prussian Carp. Additionally, the general public and fishing communities may provide an opportunity to engage in citizen science by collecting reliable data to help target areas for management (Vilà & García-Berthou, 2010).

Conclusions

Species invasions are complex and Prussian Carp's invasion in North America is no exception. Prussian Carp have only been in Alberta for 15 years, yet the rate of spread is increasing at an exponential rate over five year increments (e.g. 1.6, 2.1, and 2.3 times). The spread of Prussian Carp throughout Alberta is undoubtedly enhanced by human-assisted dispersal and the utilization of drainage canals as corridors between waterways and sub-basins.

Prussian Carp's biological characteristics such as asexual reproduction is linked to its invasiveness and dispersal ability, and it is perhaps the primary mechanism underlying Prussian Carp's invasion in western North America. Other contributing factors in its rapid spread include Prussian Carp's environmental tolerances and affinity for degraded habitats. In regions throughout Eurasia, Prussian Carp have been consistently found in degraded environments, especially in eutrophic habitats with dense aquatic vegetation. Indeed, Prussian Carp were found in the highest abundances in streams where aquatic vegetation was dense. Moreover, aquatic vegetation also came out as the most important variable in predicting Prussian Carp presence.

Although there is presently no indication that Prussian Carp are negatively affecting native species in western North America, a precautionary approach should be taken. Prussian Carp's invasion is in its infancy and there is often a considerable amount of time before changes in aquatic communities become apparent. This is particularly true for Prussian Carp and other invasive omnivores because the impacts are often indirect and manifest over long time periods (Mooney & Cleland, 2001). Prussian Carp, however, are strong competitors and their dietary requirements overlap with many species, not just in Alberta, but North America as well. This means there may be opportunities for Prussian Carp to compete or displace native species if it is better at securing certain resources. Prussian Carp may also reduce local cyprinid populations as it disperses through western North America from reproductive interference. In addition, Prussian Carp lack native predators to regulate its population; therefore, there is great potential for its population to rapidly increase and disperse uninhibited throughout western North America. Once Prussian Carp's invasion reaches a certain spatial scale, it will be challenging to quantify the impacts on local communities. Each stream likely has varying abundances and assemblages of fish species and without historical community data it will be difficult to determine Prussian Carp's effects on the local fish species.

Unfortunately, full eradication of Prussian Carp in western North America is nearly impossible but combinations of management techniques (i.e. instream barriers and piscicide on high abundance streams) may be employed to reduce the rate of spread. Prussian Carp are highly mobile and the extensive network of canals and connection between drainages poses a substantial threat to adjacent provinces and the United States. Successful management of Prussian Carp in western North America will involve the integration of all levels of government between neighbouring provincial and national borders. The collection of eDNA at Prussian Carp's invasion front can help track its movement and give managers time to prepare and employ effective management strategies. Lastly, education and involvement of the public and angling communities in management decisions will be essential as human interactions with aquatic environments can have significant influence on the future spread of Prussian Carp.

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