Management of introduced American bullfrogs (*Lithobates catesbeiana* Shaw 1802) in the South Okanagan, British Columbia

by

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Author’s declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of contributions

The data analysis, habitat suitability modeling, and writing of this thesis are the sole work of Natasha Lukey. Data collection was lead by Natasha Lukey during 2010 through 2012 field seasons, and all photos are credit Natasha Lukey unless stated otherwise. Additional contributions to this thesis include:

- Dr. Sara Ashpole and Dr. Stephen Murphy reviewed and edited this thesis;
- Dr. Sara Ashpole, Dr. Stephen Murphy, and Dr. Purnima Govindarajulu, provided thesis design and development guidance;
- Dr. Sara Ashpole, Dr. Purnima Govindarajulu, and David Cunnington secured funding and co-lead bullfrog management program design and implementation from 2004 - current.

Abstract

Introduced invasive species threaten biodiversity on a global scale. An estimated fifteen new species introduction and establishments occur in aquatic systems per decade in Canada. A particular introduced aquatic species of concern in western Canada is the American bullfrog (*Lithobates catesbeianus;* formerly *Rana catesbeiana*, Shaw 1802; hereafter referred to as bullfrogs). Bullfrogs were introduced into one wetland in the South Okanagan, British Columbia in the 1950s for human consumption, and have since been detected in 7 locations across 5 wetland complexes. Bullfrog populations were detected by biologists in the South Okanagan in 2003, and shortly after intense bullfrog control efforts were initiated. On-going, resource-intensive detection and removal efforts targeting all life stages were put into place in 2004. Limited resources and lowered detections are prompting the need to determine the potential re-colonization patterns and effort required to successfully continue to suppress populations. Determining potential colonization patterns and optimal future control measures for bullfrogs in the South Okanagan is also of critical importance to the conservation of native amphibians, 50 % of which are federally threatened, endangered, or of special concern. Introduced bullfrogs outcompete, predate upon, transmit disease to, and interfere with reproductive activity of native amphibians. The goals of this thesis were to:

1. develop a distribution model for introduced bullfrogs in the South Okanagan, to:
    a. estimate the distribution probability of bullfrogs previous to major wetland landscape changes beginning in 2004; and
    b. project the historical distribution onto the changing wetland landscape post 2004 to prioritize monitoring during average annual wetland conditions, and consecutive flood and drought years anticipated with a changing climate;
2. Analyze nine years of existing introduced bullfrog detection and removal effort in the South Okanagan, to:
    a. describe the methods, total effort, and results of the bullfrog management; and
    b. highlight key management lessons learnt through bullfrog control in the South Okanagan.

Goal 1 was addressed using species distribution modeling with Maxent®. The distribution model aimed to create a wetland-specific probability distribution for bullfrogs in the South Okanagan for 235 wetlands across a 233 km^2 extent. Hydroperiod, water velocity, surrounding matrix at 100 m, 500 m, and 1000 m, distance to nearest known breeding location, and presence of introduced predatory fish were modeled using a minimum training presence threshold to determine wetlands at highest risk of bullfrog colonization and projected onto the future wetland landscape under the 3 scenarios. Maps were validated using 28 % partitioned test data and evaluated using Area Under the Curve and True Skill Statistics. Following Maxent modeling, mapped wetlands were ranked in ArcGIS according to presence of provincially endangered or threatened native amphibian species and number of neighboring wetlands within a 1000 m buffer. Permanent, stagnant, large ponds surrounded by high cover/moisture retaining agriculture (i.e. tree fruit orchard), within 300 m of a breeding location are at highest risk of bullfrog colonization. 60.5 %, 71.5 %, and 47 % of the South Okanagan wetlands are classified for priority monitoring and carry a relative rank value of 0.5 or higher in typical, flood, and drought conditions, respectively. The resulting wetland landscape map from the present study is a water body ranked priority monitoring list for all known permanent and ephemeral wetlands in the study area. The bullfrog distribution map provides wetland criteria, and the ranked monitoring priority list highlights key areas in which to focus future bullfrog monitoring efforts within the South Okanagan.

Goal 2 was addressed using the wetland monitoring and bullfrog removal collective data set obtained from the BC Ministry of Environment, BC Ministry of Forests, Lands, and Natural Resource Operations, Environment and Climate Change Canada, and the University of Waterloo, Canada. Bullfrog detection and removal effort resulted in 11 102 introduced individual bullfrogs and egg masses detected and removed at 7 of the 125 surveyed sites in the South Okanagan between 2004 and 2012, with zero detections occurring in 2011 and 2012. Main detection and removal effort included auditory surveys, active searches, Gee trapping, and night-time canoe searches. Approximately 640 and 850 total search hours were expended for auditory and active searches respectively, and 24 670 total 24-hour trap day equivalents of Gee trapping. An additional 310 hours were spent on night-time canoe searches, 2 940 hours were spent on automated auditory recording, and 65 hours on seine netting and night-time active searches by foot. The catch per unit effort (CPUE) of the main methods varied widely among methods and sites, from 0 to 16 ± 55 individuals per trap day for Gee trapping, to 0 to 41 ± 46 individuals per search hour for active searches, and 0 to 28 individuals per hour for canoe searches. Although statistical comparison of methods is precluded due to the post-hoc nature of this analysis, results indicate that the combination of methods selected was successful in reducing abundance at the colonized ponds. However, the variation in CPUE supports the premise that effort needs to be maintained for detection and removal in subsequent years as there are likely additional individuals at low enough densities to avoid detection by standard methods. Here I recommend 10 years of zero detections, based on the Committee for the Status of Endangered Wildlife in Canada (COSEWIC)'s threatened species population trend assessment guidelines. Major lessons learned include: each water body requires an adaptive and robust approach; removal efforts must be persistent; future monitoring should focus on a slight increase in visual effort and slight reduction in auditory effort when populations are at low abundances; and repetitive training is required for observers to ensure accurate identification. The future of bullfrog control in the South Okanagan presents challenges under low population abundance and low detectability, and reduced funding while population suppression is at a critical point in preventing re-establishment. Multiple collaborative efforts combining different agency goals and target species is recommended to help alleviate the resource-limiting pressure for monitoring.

Ultimately, the results of this thesis suggest permanent, stagnant, ponds surrounded by high cover/moisture retaining agriculture (i.e. tree fruit orchard), within 300 m of a breeding location are at highest risk of bullfrog colonization, and monitoring should focus on a slight increase in visual effort and slight reduction in auditory effort when populations are at low abundances.

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List of Acronyms

Acronym	Definition
	Organizations
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
DFO	Department of Fisheries and Oceans Canada
DUC	Ducks Unlimited Canada
ECCC	Environment and Climate Change Canada (formerly Environment Canada)
HCTF	Habitat Conservation Trust Fund
ISCBC	Invasive Species Council of BC
ISSG	Invasive Species Specialist Group
MOE	BC Ministry of Environment
MOFLNRO	BC Ministry of Forests, Lands, and Natural Resource Operations
OIB	Osoyoos Indian Band
OSCA	Okanagan Similkameen Stewardship Society
OSS	Okanagan Similkameen Stewardship Society, formerly with TLC The Land Conservancy BC
SOSCP	South Okanagan Conservation Program
TNTBC	The Nature Trust BC
	Technical terms
AUC(ROC)	Area Under the Curve (Receiver Operator Characteristic)
BD	*Batrachochytrium dendrobatidis*
BIOCLIM	Bioclimatic Niche Model
ENT	Ecological Niche Theory
GAM	Generalized Additive Model
GARP	Genetic Algorithm for Rule-set Prediction
GLM	Generalized Linear Model
GSID	Global Invasive Species Database
HSM	Habitat Suitability Model
MaxENT	Maximum Entropy
SARA	Species At Risk Act
SOWMA	South Okanagan Wildlife Management Area
TSS	True Skill Statistic

Chapter 1: Literature Review

1.1 Introduction

Introduced invasive species threaten biodiversity on a global scale (McGeoch et al. 2010). Introduced invasive species result when organisms are accidentally or intentionally transported across an ecologically relevant distance or natural dispersal barrier, and subsequently establish, disperse, and inflict negative impacts on native species and habitat (McGeoch et al. 2010). Introduced invasive species encompass all kingdoms and are detrimental to environmental, economic, and societal health. Impacts of invasive species are direct, including transmission of disease to humans and native organisms, or indirect, including destruction of infrastructure, food, and other resources relied heavily upon by humans and native organisms (Invasive Species Council of BC (ISCBC) 2012). Introduced invasive species cost local governments and agencies billions in prevention, control, and infrastructure and ecosystem damage. Sixteen federally regulated invasive species alone cost the Canadian economy an estimated $CDN 13 - 34 billion annually, before fully considering effects on local ecosystems (Richardson 2008). Introduced invasive species cost the United States an estimated $USD 120 billion annually when considering prevention programs, ecosystem effects, and invasive species-induced harvest loss and infrastructure repairs (Pimentel et al. 2005).

Anthropogenic vectors are the main pathway of foreign species introduction into new environments (Ficetola et al. 2007(a), Jeschke and Strayer 2006). Humans facilitate population establishment and dispersal by modifying native environments (Crooks and Soule 2001). Agricultural landscapes are a prime example of land use modifications and degradation resulting in introduced species invasions (Sakai et al. 2001). Agricultural systems involve disturbed land, and wetlands and ephemeral ponds converted into permanent, sparsely vegetated ponds ideal for colonization by introduced plants and animals (Sakai et al. 2001).

Aquatic systems, including remnants within agroecosystems, are particularly vulnerable to impacts of introduced invasive species (Dudgeon et al. 2006). An estimated fifteen new species introduction and establishments occur in aquatic systems per decade in Canada (Department of Fisheries and Oceans Canada (DFO) 2004). A particular introduced aquatic species of concern, often associated with agricultural landscapes, is the introduced, invasive American bullfrog (*Lithobates catesbeiana* Shaw [= *Rana catesbeiana* Shaw]; herein referred to as bullfrog). Bullfrogs are used for human consumption, in ceremonial wildlife release, and research in consumer goods and amphibian ecology and toxicology (Global Invasive Species Database (GISD) 2005, Huang et al. 2014, Liu et al. 2012). The popularity of bullfrogs for human use has led to their widespread translocation and establishment outside of their native range of eastern North America (Figure 1.1.1). The diverse and negative impacts introduced bullfrogs exert on native diversity has led to the bullfrog species' listing among the world's top 100 "worst invaders" (Lowe et al. 2004).

Figure 1.1.1 Global distribution of American bullfrogs. Yellow region indicates native range; red circles indicate introduced populations; black circles indicate introduced British Columbia populations. Introduced bullfrog populations have been recorded on all continents except Antarctica, Africa, and Australia (Global Invasive Species Database 2005). World map adapted from Wikimedia Commons (2011) and distribution data obtained from the Global Invasive Species Database (2005).

Bullfrogs were introduced into one wetland in the South Okanagan, British Columbia in the 1950s for human consumption (K. Faverholdt, pers. comm.), and have since been detected in 7 locations (Lukey et al. 2012). Bullfrog populations were detected by biologists in the South Okanagan in 2003, and shortly after intense bullfrog control efforts were initiated. On-going, resource-intensive detection and removal efforts targeting all life stages were put into place in 2004 (Lukey et al. 2012). Limited resources and lowered detections are prompting the need to determine the potential re-colonization patterns and effort required to successfully continue to suppress populations. Determining potential colonization patterns and optimal future control measures for bullfrogs in the South Okanagan is also of critical importance to the conservation of native amphibians, 50 % of which are federally threatened, endangered, or special concern (Species At Risk Act (SARA)). The following literature review discusses the invasive capacity and impacts of introduced bullfrogs, management measures for introduced bullfrogs, and the implications of introduced bullfrogs in the South Okanagan.

1.2 Life history characteristics strengthening the American bullfrog's invasion capacity

Population declines in the bullfrog's native range are documented since the mid-1900s (Hecnar and M'Closkey 1997, Willis et al. 1956) and are attributed to habitat degradation and over-harvesting (Flores-Nava 2002, Schmutzer 2008, Spear et al. 2009, Willis et al. 1956). Despite sensitivities within their native range, bullfrogs are capable of rapidly colonizing and persisting in new environments. Multiple life history characteristics and ecological interactions within the bullfrogs' native range contribute to the invasive capacity of bullfrogs in new environments:

Size: Bullfrogs are now North America's largest anuran, reaching just under 20 cm snout-to-vent (Shirose and Brooks 1995, Willis et al. 1956). The large size of the larvae and transformed individuals in comparison to other native species enables bullfrogs to consume a diverse selection of prey size and type, and confers competitive advantages.

Omnivorous, generalist diet: Bullfrogs consume algae, insects, snakes, turtle hatchlings, birds, salamanders, small mammals, and most commonly, other frogs (Bruneau and Magnin 1980, Clarkson and deVos 1986, Govindarajulu et al. 2006, Korschgen and Moyle 1955, Sloan and Marks 2012, US Fish and Wildlife 2002).

Habitat generalists: Bullfrogs exhibit preference for permanent, warm water bodies with abundant woody litter and bank vegetation with open spaces (Cunningham et al. 2007, Lichtenberg et al. 2006). However, reproductively successful introduced bullfrog populations occur in highly degraded water bodies with sparse to no vegetation, water bodies as small as 1.5 m diameter, slow-moving streams, and faster flowing river backwaters (Carl and Cowan 1945, Fuller et al. 2011, Graves and Anderson 1987, Nie et al. 1999). Agricultural landscapes with ponds and introduced predatory fish are also highly correlated with introduced bullfrog populations (Li et al. 2006, Bunnell and Zampella 2008, D'Amore et al. 2010, Maret et al. 2006).

Reproductive capacity: Bullfrogs lay up to 25 500 eggs per season per female (Govindarajulu et al. 2004, Wright 1914). Female bullfrogs typically breed once per year, but breed twice per year in some introduced areas (Clarkson and deVos 1986, Leivas et al. 2012). Bullfrogs establish viable populations with low founding genetic diversity (Bai et al. 2012, Ficetola et al. 2008(a)). Invasive bullfrog populations across Europe are attributed to less than 6 founding females, and potentially only 2 females and 1 male in Italy (Ficetola et al. 2008(a)). Introduced bullfrog populations also retain high genetic diversity relative to native populations (Funk et al. 2011). High reproductive capacity of bullfrogs may facilitate selection against deleterious alleles in founding populations, limiting negative population viability effects from inbreeding depression (Bai et al. 2012, Facon et al. 2011, Perez et al. 2012, Wang 2000).

Natural dispersal: Bullfrogs are capable of overland movements of 1000 m per year in their native range (Corse and Metter 1980, Ingram and Raney 1943, Willis et al. 1956). Rapid dispersal has been observed in invading ranges, with movement distances and range expansion up to 5 km per year (Govindarajulu 2004). Dispersal occurs primarily within water channels and riparian areas, but can also occur across agricultural environments, roads, and dry, harrowed fields (Willis et al. 1956, Youngquist and Boone 2012).

Ecological influence: Bullfrogs shape and dominate their native communities (Boone et al. 2004, Hecnar and M'Closkey 1997, Werner 1994, Werner and McPeek 1994). Bullfrogs influence survival and mass at metamorphosis of sympatric amphibian species (Boone et al. 2004, Werner 1991, Werner 1994). Bullfrog tadpoles increase rates of unpalatable macrophyte production (Werner 1994), decrease rates of primary production by phytoplankton, reduce rates of nitrogen fixation by blue-green algae, and transport nutrients from ponds to terrestrial systems upon metamorphosis (Seale 1980). Bullfrogs are also valuable prey and host animals for a variety of organisms, and key players in interspecific and intraspecific predatory and competitive relationships (McAlpine and Dilworth 1989, Stewart and Sandison 1972, Werner and McPeek 1994, Werner 1994).

1.3 Impacts of introduced American bullfrogs in foreign environments

In many regions where introduced bullfrogs are present, anecdotal and scientific evidence suggest native amphibian populations are declining (Hayes and Jennings 1986, Kupferberg 1997, US Fish and Wildlife 2002). Specific mechanisms by which bullfrogs affect native species are identified in many parts of the bullfrog's introduced range (Adams 1999, Blaustein and Kiesecker 2002, Hayes and Jennings 1986, Li et al. 2011(b)):

Predation: bullfrogs are voracious predators, particularly towards frogs (Boelter et al. 2012, Bruneau and Magnin 1980, Kiesecker and Blaustein 1997, Stewart and Sandison 1972, Werner et al. 1995, Wu et al. 2005). Bullfrogs may predate certain species more heavily depending on their use of microhabitat or predator evasion tactics (Pearl et al. 2004). Within species, smaller adults are more susceptible to predation by adult bullfrogs (Wang et al. 2007), and native eggs are susceptible to predation by tadpoles (Ruibal and Laufer 2012).

Competition and influence on resources: The generalist diet of bullfrogs overlaps with native insectivores, algivores, and small animal carnivores (Ruibal and Laufer 2012, Wu et al. 2005). Bullfrogs out-compete other organisms for food (Boone et al. 2004, Kiesecker and Blaustein 1997, Kiesecker et al. 2001, Kupferberg 1997), and affect nutrient cycling in water bodies by depleting algal resources (Kupferberg 1997, Pryor 2003, Ruibal and Laufer 2012, Seale 1980).

Disease transmission: Bullfrogs are vectors for the chytrid fungus, *Batrachochytrium dendrobatidis* (BD) (Bai et al. 2010, Gahl et al. 2012, Garner et al. 2006, Greenspan et al. 2012, Hanselmann et al. 2004, Schloegel et al. 2012). Chytridiomycosis caused by BD is responsible for mass die-offs of amphibian populations around the world (Kilpatrick et al. 2011, Lips et al. 2006, Rachowicz et al. 2006, Wake 2012). Although strains of BD may be endemic to a bullfrog's introduced range, bullfrogs carry novel strains of BD to the introduced range, putting naïve native amphibians at risk of infection (Schloegel et al. 2012). Bullfrogs also act as reservoirs for ranaviruses responsible for amphibian die-offs (Mazzoni et al. 2009, Miller et al. 2011, Sharifian-Fard et al. 2011).

Influence fitness and behavior of native amphibians: In the presence of bullfrogs, native individuals shift microhabitat use (Kiesecker et al. 2001), engage in interspecific amplexus, and change mate calling frequencies (Both and Grant 2012, D'Amore et al. 2009, Pearl et al. 2005(b)).

Synergistic interactions with other threats: Anthropogenic habitat modification may favor bullfrog colonization in areas where habitat is fragmented (D'Amore et al. 2010, Hager 1998), or ephemeral wetlands are converted and permanent water bodies created for human use (Adams 1999, Bunnell and Zampella 2008, D'Amore et al. 2010, Hayes and Jennings 1986, Maret et al. 2006). Introduced predatory fish species facilitate bullfrog colonization (Adams et al. 2003, Boone and Semlitsch 2003, Kiesecker and Blaustein 1997, Werner and McPeek 1994). Invasive *Phragmites australis*, destructive to native communities (Meyerson et al. 2000), also facilitates the growth and survival of bullfrog tadpoles (Clarkson and deVos 1986, Rogalski and Skelly 2012). Finally, algae species associated with algal blooms in degraded wetlands are correlated with rapid bullfrog tadpole growth, and are easily exploited and digested by bullfrog tadpoles (Pryor 2003, Seale 1980).

1.4 Prevention and control of introduced American bullfrog populations

The widespread invasion of bullfrogs has prompted multiple control and removal efforts in various parts of the world. Documented introduced bullfrog management programs have occurred in Europe (Foster and Banks 2008, Kraus 2009, Louette et al. 2014, Marchant 2012, Nehring and Klingenstein 2008, Reinhardt et al. 2003, Spitzen-van der Sluijs and Zollinger 2010), the western United States (Kraus 2009, Schwalbe and Rosen 1988, Adams and Pearl 2007, US Fish and Wildlife 2002), the Lower Mainland, BC (Orchard 2011), and the South Okanagan, BC (Lukey et al. 2012). The cost and success for eradication varies with bullfrog density, size, shore vegetation complexity, and methods of detection and removal (Adams and Pearl 2007, Kraus 2009, Orchard 2011). Bullfrog control and removal efforts can be upwards of $ 70 000 CDN per water body (Nehring and Klingenstein 2008, Orchard 2011, Reinhardt et al. 2003).

Many bullfrog control programs have lacked long-term follow-up monitoring to determine true eradication success, likely due to limited funding (Krauss 2009). A common issue in invasive species management is the cessation of funding from supporting agencies once target species are deemed to be in low enough densities to no longer be impacting the native environment (Simberloff 2005). Programs that have failed at eradication attempts have also failed because of a combination of factors: dense and wide-ranging bullfrog populations; complex wetland vegetation structure; failure to detect and remove all life stages; and low human power and financial resources (Hull and Rushton 2012, Krauss 2009). The programs resulting in eradication include localized bullfrog populations in relatively simple wetland vegetation structure, and intense monitoring (Adams and Pearl 2007, Foster and Banks 2008, Kraus 2009, Simberloff

2005, Spitzen-van der Sluijs and Zollinger 2010). Successful introduced bullfrog eradication programs are also adaptive, employing predictive habitat modeling, constantly assessing resource use, investigating invasion pathways, triggering or relying on legislation restricting bullfrogs, and public education (Adams and Pearl 2007, Foster and Banks 2008, Kraus 2009, Simberloff 2005, Spitzen-van der Sluijs and Zollinger 2010).

Common methods used in bullfrog management programs include habitat suitability modeling (HSM) and removal effort analysis. Habitat risk prediction and effort analysis are vital to developing adaptive management programs for invasive species, and are used before or after the introduction of a species into a new region. Habitat suitability modeling attempts to predict a species' range using presence data, from introduced and/or native habitat, and ecological niche information (Franklin 2009). Habitat suitability modeling can be used to estimate range extent prior to a species' introduction, predict range expansion after introductions, or to infer environmental variables likely to limit establishment (Crossman et al. 2011, Franklin 2009, Gormley et al. 2011, Pyron et al. 2008, Ron 2005, Thuiller et al. 2005). Multiple HSM models exist, each with varying assumptions, strengths, limitations, and data requirements; however, all are based on the Ecological Niche Theory (ENT) (Franklin 2009, Guisan and Thuiller 2005). The ENT assumes that individuals' fitness is tightly linked to their environment; therefore, organisms can only operate within specific environmental boundaries (Grinnell 1917, Hirzel and Le Lay 2008). Section 1.6 of this chapter examines the relevance of various models to the bullfrog management program in the South Okanagan, and Chapter 2 of this thesis aims to create a habitat suitability model for bullfrogs in the South Okanagan.

Complementary to habitat suitability modeling is continuously evaluating how human and financial effort is spent, where it may be lacking, and efficacy of methods (Leung et al. 2002, Pichancourt et al. 2012, Wise et al. 2012). Effort analysis can be used to balance the cost of eradication techniques with the sensitivity of life stages on population viability, or to determine whether control efforts are best allocated to population control or prevention of subsequent introduction and spread (Leung et al. 2002, Pichancourt et al. 2012). Effort analysis is used either at the onset of a management program to decide end goals or management methods, or prospectively to redefine or confirm end goals and management methods (Pichancourt et al. 2012, Wise et al. 2012). Published information regarding effort input in invasive bullfrog population management around the globe is limited, and no effort analysis has been conducted on introduced bullfrog management in the South Okanagan. Chapter 3 of this thesis examines the capture effort for bullfrogs in the South Okanagan, BC from 2004 to 2012.

1.5 Potential impacts of introduced American bullfrogs in the South Okanagan

Previous research in other regions about bullfrog invasions can give insight into the vulnerability of the South Okanagan community, and potential impacts of invasions in the South Okanagan. The Canadian range of the South Okanagan extends from Peachland, BC, to the USA border at the south. The valley sits between mountain regions to the east and west, and is connected north-to-south by large lakes, the Okanagan River, and floodplain along the valley bottom. The elevation and climate of the mountain ranges bordering the region may help shield the area from non-human facilitated bullfrog range expansion (Li et al. 2011(a), Nori et al. 2011), particularly from coastal BC colonies and newly documented populations across the eastern mountains, immediately south of the US border from the Kootenay region of BC (B. Houston pers. comm.). However, recent reports of bullfrogs in the Central Okanagan (P. Govindarajulu pers. comm.), little knowledge of populations directly across the US-Canada border, and established populations further south in Washington, Oregon, and California (GISD 2005, Pearl et al. 2005(a), US Fish and Wildlife 2002), raise concerns for natural dispersal into the South Okanagan from the north and south. The South Okanagan is also a main travel vector from the coast across Canada, and is a popular tourist location, increasing risk of human-facilitated bullfrog introductions.

1.5.1 Implications of introduced American bullfrogs for native South Okanagan amphibians

The South Okanagan is home to 6 native amphibian species, 3 of which are federally listed as endangered, threatened, or of special concern (Table 1.5.1).

Table 1.5.1 South Okanagan amphibian species and their Provincial[1], Federal Species At Risk Act (SARA)[2], and Committee on the Status of Endangered Wildlife in Canada (COSEWIC)[3] listing.

Species name	Provincial listing	Federal listing	COSEWIC listing
Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*)	Red	Endangered	Endangered
Long-toed Salamander (*Ambystoma macrodactylum*)	Yellow	Not listed	Not At Risk
Western Toad (*Anaxyrus boreas*)	Blue	Special Concern	Special Concern
Great Basin Spadefoot (*Spea intermontana*)	Blue	Threatened	Threatened
Pacific Treefrog (*Pseudacris regilla*)	Yellow	Not listed	Not listed
Columbia Spotted Frog (*Rana luteiventris*)	Yellow	Not listed	Not At Risk
*Northern Leopard Frog (*Lithobates pipiens*)	Red	Endangered	Endangered

*Extirpated in Okanagan Region

The level of threat from introduced bullfrogs faced by each South Okanagan native species varies based on current population status, occurrence in low elevation wetlands, susceptibility to chytrid fungus, water permanency requirements, peak breeding times, time to metamorphosis, body size, and adaptability to introduced predatory fish (Table 1.5.2). Bullfrogs are more fecund than all the native amphibian species, much larger in every life stage with the exception of older

[1] www.env.gov.bc.ca/atrisk/red-blue.htm
[2] www.ec.gc.ca/alef-ewe/default.asp?lang=en&n=ED2FFC37-1
[3] www.cosewic.gc.ca/eng/sct6/index_e.cfm

Tiger salamanders, and all the native amphibian species are vulnerable to introduced predatory fish. Early spring breeding patterns and the ability of most South Okanagan amphibians to breed in ephemeral ponds may provide a temporal and spatial buffer against encounters with later emerging and breeding bullfrogs, assuming bullfrogs continue to follow the mid-June breeding patterns previously observed in the South Okanagan and Vancouver Island (Govindarajulu et al. 2006, S. Ashpole unpublished data). However, bullfrogs may have the potential to breed in April, as observed in California, Arizona, and historically in southwestern BC (Carl and Cowan 1945, Clarkson and deVos 1986). Bullfrog tadpoles also overwinter, putting early emerging and hatching native South Okanagan amphibians at risk of encountering the previous year's bullfrog tadpoles.

Predation impacts at the population scale for native species may also vary based on breeding hydroperiod requirements. Ephemeral ponds may act as stepping stones during bullfrog dispersal, but may not be consistently colonized annually. Once introduced, permanent ponds likely would be colonized annually by bullfrogs, putting species such as Tiger Salamanders at a higher risk of impact on a population level due to exposure time with bullfrogs.

Apart from body size and sensitivity to introduced predatory fish, each of the South Okanagan amphibian species embodies a different set of life history characteristics which put them at varying risk to bullfrogs. Based on information regarding bullfrog impacts in other regions, and the species-specific life history, Tiger Salamanders and Western Toads are perceived to be at highest risk, Long-toed Salamanders, Pacific Treefrogs and Columbia Spotted frogs at medium risk, and Great Basin Spadefoots at lower risk of negative impacts from introduced bullfrog populations (Table 1.5.2).

Table 1.5.2 South Okanagan native species' potential level of risk of negative impacts from introduced bullfrogs. Risk level is estimated based on life history characteristics and provincial population status. Blotched Tiger Salamanders and Western Toads are at highest level risk from introduced bullfrogs.

Native Species	Potential life history advantages	Potential life history disadvantages	*Potential risk level	Relevant literature
Blotched Tiger Salamander	- Predate bullfrogs - Use longer-lasting ephemeral water bodies - Ambystomids show resistance to chytrid infection from native environments; however, lethality of foreign *Batrachochytrium dendrobatidis* (BD) infection is unknown	- Permanent water bodies required for population persistence - Sensitive to fish-invaded waters; fish impacts increased by bullfrogs - Predated upon by bullfrogs - Breeding season occurrence overlap with bullfrogs - Salamander population abundance is negatively correlated with introduced bullfrog presence	High	BC MOE (2013); Boone et al. (2008); Davidson et al. (2003); Fisher and Shaffer (1996); Jennings and Hayes (1994); Kats and Ferrer (2003); Maret et al. (2006); Pilliod (2013); Richardson et al. (2000); Werner and McPeek (1994)
Western Toad	- Use ephemeral water bodies; decreased potential for temporal overlap with adult bullfrogs - Aquatic only during egg/tadpole stage and during breeding	- Anaxyrus species highly susceptible to lethal BD infections -Bullfrogs reduce Toad survival in mesocosm experiments - Require 1.5 to 3 months for transformation, increasing likelihood of occurrence overlap with bullfrogs	High	BC Conservation Data Center (2013); BC MOE (2013); Boone et al. (2008); Deguise and Richardson (2009); Olson (2005)
Long-toed Salamander	- Use ephemeral water bodies - Ambystomids show resistance to chytrid infection from native environments; however, lethality of foreign Batrachochytrium dendrobatidis (BD) infection is unknown	- Use permanent water bodies - Species-specific chytrid effects unknown - Potential for predation by bullfrogs - Transform mid to late summer: potential occurrence overlap	Medium	BC MOE (2013); Bull (2005); Davidson et al. (2003); Pearl et al. (2005(a)); Pearson and Goater (2008); Pilliod (2013)

*Potential Level of risk to native species from introduced bullfrogs based on habitat requirements, breeding and pond occupation time, population status, and susceptibility to lethal BD infection, predation, and competition from bullfrogs.

Table 1.5.2. continued... South Okanagan native species' potential level of risk of negative impacts from introduced bullfrogs. Risk level of risk is estimated based on life history characteristics and provincial population status. Blotched Tiger Salamanders and Western Toads are at highest level risk from introduced bullfrogs.

Native Species	Potential life history advantages	Potential life history disadvantages	*Potential risk level	Relevant literature
Columbia Spotted Frog	- Prefer slow-running streams at higher elevation - Show resistance to chytrid infection from native environments, though foreign (BD) infection lethality unknown	- Use permanent water bodies Very similar in appearance to young bullfrogs, bullfrog eggs, and tadpoles; at major risk for misidentification as bullfrogs	Medium	BC MOE (2013);Russell et al. (2010); Somaweera et al. (2010)
Pacific Treefrog	- Able to persist in many bullfrog-invaded habitats despite declines in some regions	- Bullfrog co-occurrence results in reduced survival from competition, predation, and reduced resource intake in bullfrog presence - Bullfrog effects difficult to predict and vary with study scale, microhabitat, and resource availability - BD may have sub-lethal impacts on individuals, reducing annual recruitment	Medium	Adams (2000); BC MOE (2013); Govindarajulu (2004); Kleinhenz et al. (2012); Kupferberg (1997)
Great Basin Spadefoot	- Use ephemeral water bodies; decreased potential for occurrence overlap with bullfrogs - Fossorial and terrestrial except during breeding in spring/summer	- Some occurrence overlap with dispersing bullfrogs in ephemeral water bodies - Susceptibility to lethal BD infections unknown	Low	Balfour and Morey (1999); BC MOE (2013); Cunningham et al. (2007); Gahl et al. (2009); Hallock (2005); Ruibal et al. (1969);

*Potential level of risk to native species from introduced bullfrogs based on habitat requirements, breeding and pond occupation time, population status, and susceptibility to lethal BD infection, predation, and competition from bullfrogs.

1.6 Examining introduced bullfrog management in the South Okanagan

Introduced bullfrogs are the subject of multiple HSMs, in multiple regions around the world (Ficetola et al. 2007(b), Ficetola et al. 2010, Giovanelli et al. 2008, Nori et al. 2011). However, all previously published HSMs for bullfrogs are on large regional to global scales (Ficetola et al. 2007(b), Ficetola et al. 2010, Giovanelli et al. 2008, Nori et al. 2011). The research presented in Chapter 2 of this thesis creates an HSM for bullfrogs at the pond-based scale.

A major consideration when modeling species' ranges is the type of presence data available and the limitations of each data type. Common HSM models include Maximum Entropy (MaxENT), Habitat Suitability Index, Bioclimatic Envelope, Genetic Set-rule Production, Ecological Niche Factor, Generalized Additive, and Generalized Linear (Table 1.6.1). The applicability of each model method to predicting bullfrog habitat suitability in the South Okanagan varies given the nature of available data for bullfrog populations in the South Okanagan, and each modeling method's requirements and scale suitability (Table 1.6.1). The large number of water bodies in the study area requiring data for modeling limits the type of predictor variables that can be used, such as temperature profiles. However, multiple relevant wetland predictor variables exist which are important to bullfrog population persistence, including: hydroperiod (Cunningham et al. 2007, D'Amore et al. 2010); water velocity (D'Amore et al. 2010, Fuller et al. 2011); surrounding landscape matrix and distance from other water bodies (Currie and Bellis 1969, D'Amore et al. 2010, Ingram and Raney 1943); distance to breeding locations (Ingram and Raney 1943, Raney 1940), and introduced predatory fish presence (Adams et al. 2003, Cunningham et al. 2007, Werner and McPeek 1994). Of all the HSM methods, Maximum entropy is most consistent with the South Okanagan bullfrog modeling data categories, scale, and ability to provide insight into predictor variable importance to bullfrogs in the South Okanagan (Table 1.6.1).

Table 1.6.1 Habitat suitability modeling method compatibility for introduced bullfrogs in the South Okanagan. Maximum entropy and habitat suitability index modeling are the most appropriate methods. Crosses (X) indicate compatibility. Value 5 = highest relevance (Table adapted from Lukey 2011).

Method	Small scale	Presence-only	Categorical data	Invasive species	Limited occurrence data	*Relevance level
Maximum entropy	X	X	X	X	X	5
Habitat suitability index	X	X	X	X	X	5
Bioclimatic envelope		X	X	X		3
Genetic rule-set production		X	X			2
Ecological niche factor		X			X	2
Generalized additive			X			1
Generalized linear			X			1

*Relevance level: assigned to each habitat suitability model based on model criteria required and data available for South Okanagan. Criteria required are assumed equal value and additive.

The South Okanagan bullfrog management also includes an extensive database with management effort and capture returns (S. Ashpole et al., unpublished). This database is employed in Chapter 3 to compliment the HSM and inform management decisions regarding where and what types of effort are recommended for future bullfrog management.

1.6.1 South Okanagan bullfrog management relative to Provincial introduced species management

The Invasive Species Council of BC (ISCBC 2012) recently proposed the Invasive Species Strategy, broadening the recommended scope of introduced species management in BC. Specific policy for bullfrogs is not written into the strategy; however, the scope of the strategy does include aquatic invasive species (ISCBC 2012). The Invasive Species Strategy (2012) addresses three key challenges and six solutions required for invasive species mitigation in BC. This thesis research will address 2 of the three challenges, and 4 of the 6 proposed solutions defined by the Invasive Species Strategy (ISCBC 2012; Table 1.6.2). The habitat suitability model and effort analysis will address the Strategy's (ISCBC 2012) defined challenges associated with funding capacity and longevity, and examining and addressing invasion pathways.

Table 1.6.2 Challenges and solutions for alien invasive species management in British Columbia, proposed by the BC Invasive Species Council's (2012) Invasive Species Strategy, directly addressed in this research.

Challenges	Addressed by thesis research?
1. Insufficient funding, capacity, and research	Yes
2. Invasion pathways and vectors	Yes
3. Increasing impacts	No
Proposed solutions	
1. Build strong collaboration	Yes
2. Prevent introduction and spread	Yes
3. Implement effective control, restoration, and monitoring programs	Yes
4. Conduct relevant and applicable research	Yes
5. Provide stable, long-term funding	No
6. Establish and enforce effective regulatory tools	No

1.7 Conclusion

Introduced bullfrogs pose a direct threat to South Okanagan native amphibians. The large size, fecundity, and generalist life characteristics make bullfrogs a formidable competitor and predator for the less fecund, smaller native amphibian species. Although some bullfrog colonized regions may need to consider containment and acceptance of bullfrog populations, the South Okanagan contains small, localized water bodies which potentially facilitate bullfrog eradication (Foster and Banks 2008, Govindarajulu 2004, Hull and Rushton 2012). To ensure long-term success of bullfrog population suppression, current physical detection and removal efforts must be combined with effort analysis, habitat suitability modeling in an adaptive management approach.

The following thesis research will address the lack of adaptive management in the South Okanagan for bullfrogs by creating a habitat suitability map and analyzing control effort resources to date. The habitat suitability map and effort analysis will be used to refine management decisions and provide recommendations for the future of bullfrog population suppression in the South Okanagan. This thesis research also aligns with BC provincial invasive species goals defined in the Invasive Species Strategy for BC (ISCBC 2012), and will directly contribute to research and management of invasive species in the province.

Chapter 2: Distribution modeling for introduced invasive American Bullfrogs (*Lithobates catesbeianus* (Shaw, 1802; Ranidae)) in the South Okanagan, British Columbia

Overview

Introduced American bullfrogs (*Lithobates catesbeianus;* formerly *Rana catesbeiana*, Shaw 1802) are a globally invasive species which pose a threat to native amphibian species. Introduced bullfrogs outcompete, predate upon, transmit disease to, and interfere with reproductive activity of native amphibians. Bullfrogs were introduced into the South Okanagan in the 1950s, but were not detected by biologists until 2003. Immediately following detection, on-going control efforts were launched which have reduced bullfrog detections to 0 individuals of all life stages since 2011. The next phase in bullfrog control is developing methods to assist decision-making for allocating monitoring effort given the possibility for potentially remaining, undetected individuals, or additional human-facilitated introductions. The goal of this paper was to develop a distribution model for introduced bullfrogs in the South Okanagan. Specifically, I aimed to: 1) estimate the distribution probability of bullfrogs previous to major wetland landscape changes beginning in 2004; and 2) project the historical distribution onto the changing wetland landscape post 2004 to prioritize monitoring during: average annual wetland conditions; and consecutive flood and drought years anticipated with changing climate. Species distribution modeling using Maxent® was conducted to create a wetland-specific probability distribution for bullfrogs in the South Okanagan for 235 wetlands across a 233 km^2 extent. The model extent was limited to all permanent and ephemeral wetlands for which environmental predictor variable data was known. Hydroperiod, water velocity, surrounding matrix at 100 m, 500 m, and 1000 m, distance to nearest known breeding location, and presence of introduced predatory fish were modeled using a minimum training presence threshold to determine wetlands at highest risk of bullfrog colonization and projected onto the future wetland landscape under the 3 scenarios. Maps were validated using 28 % partitioned test data and evaluated using Area Under the Curve and True Skill Statistics. Following Maxent modeling, mapped wetlands were ranked in ArcGIS according to presence of provincially endangered or threatened native amphibian species and number of neighboring wetlands within a 1000 m buffer. Permanent, stagnant, large ponds surrounded by high cover/moisture retaining agriculture (i.e. tree fruit orchard), within 300 m of a breeding location are at highest risk of bullfrog colonization. 60.5 %, 71.5 %, and 47 % of the South Okanagan wetlands are classified for priority monitoring and carry a relative rank value of 0.5 or higher in typical, flood, and drought conditions, respectively. The resulting wetland landscape map from the present study is a water body ranked priority monitoring list for all known permanent and ephemeral wetlands in the study area. The bullfrog distribution map provides wetland criteria, and the ranked monitoring priority list highlights key areas for which to focus future bullfrog monitoring efforts within the South Okanagan.

Introduction

American bullfrogs, *Lithobates catesbeiana* Shaw (formerly *Rana catesbeiana* Shaw*;* hereon referred to as bullfrogs), are listed among the world's top 100 most invasive species by the International Union for the Conservation of Wildlife (Lowe et al. 2004). Native to eastern North America, bullfrogs have been introduced and become established on 4 continents (Global Invasive Species Database 2015). Native, ecologically naïve amphibian species are most vulnerable to introduced bullfrogs. Introduced bullfrogs outcompete (Kiesecker et al. 2001, Kupferberg 1997, Wu et al. 2005), predate upon (Kiesecker and Blaustein 1997, Wu et al. 2005), transmit disease to (Garner et al. 2006, Mazzoni et al. 2009, Schloegel et al. 2012), interfere with reproductive activity of (D'Amore et al. 2009, Pearl et al. 2005(b)), and act in synergy with introduced predatory fish and chemical pollutants to amplify pressure on native amphibians (Adams et al. 2003, Boone et al. 2007, Maret et al. 2006).

Bullfrogs were introduced to the South Okanagan, British Columbia, in the 1950s for food production (K. Favrholdt pers. comm.). The South Okanagan is home to 6 amphibian species, 3 of which are provincially listed as threatened or endangered: Blotched Tiger Salamanders (*Ambystoma mavortium melanostictum*); Great Basin Spadefoots (*Spea intermontana*); and Western Toads (*Anaxyrus boreas*) (BC Ministry of Environment 2013). Many amphibian species in the South Okanagan occur at the northern extent of their species' range; populations at the periphery of a species' range may harbor genetic variability not found in the core of that species' range (Lesica and Allendorf 1995). In a landscape with over 84 % wetland and riparian habitat lost to development or anthropogenic modification (Lea 2008), a variety of agricultural and urban aquatic pollutants (Bishop et al. 2010), and heavy landscape fragmentation, introduced bullfrogs pose additional threat to native amphibian survival. Bullfrog invasion is human-facilitated, and regional population establishment can occur with low founding genetic diversity and as few as 3 individuals (Bai et al. 2012, Ficetola et al. 2008(a)). In addition to being critical to native amphibian conservation, continued bullfrog monitoring in the South Okanagan is also important in the face of a changing wetland landscape within the South Okanagan. The drastic loss of over 84 % of South Okanagan wetland and riparian habitat since the early 1900s (Lea 2008) has resulted in local organizations reconstructing and enhancing terrestrial habitat and water bodies throughout the bullfrog-infected area over the past decade. Bullfrogs are common colonizers of newly restored and enhanced open-water wetlands, particularly during early stages of native vegetation succession and wildlife community establishment (Balcombe et al. 2005, Palis 2007, Pearson and Mooney 2012, Shulse et al. 2010). Many of the restored and constructed water bodies in the South Okanagan are suspected suitable breeding or dispersal corridor habitat for newly introduced or remaining undetected bullfrogs. Monitoring the recently constructed wetlands in the South Okanagan for bullfrog colonization is important in balancing the increased short-term risk of bullfrog colonization with long-term goals of habitat restoration for native species in newly constructed wetlands.

Efficiently monitoring for native amphibians and introduced bullfrogs in the South Okanagan is challenging due to the difference in timing of the active breeding seasons of native amphibians and bullfrogs. Though bullfrogs were introduced in the 1950s, the populations were not detected by scientists until 2003 due to temporal disparity between native South Okanagan amphibian and bullfrog surveys, and low survey effort on private land. Bullfrog population control efforts were implemented immediately following detections. Control efforts included a diversity of trapping methods, exclusion fencing to prevent dispersal from high-density ponds, and repeated surveys to assess removal success and dispersal to neighboring ponds. Bullfrog detections have been reduced to 0 detections since 2011, potentially indicating that this population has been functionally eradicated (Lukey et al. 2012). However, re-colonization can occur by remaining undetected individuals and potential subsequent new human-facilitated introductions to the region. The next phase of bullfrog management in the South Okanagan is developing methods to inform and optimize future bullfrog monitoring efforts. Distribution modeling for bullfrogs can facilitate resource allocation decisions by determining high-risk wetlands and prioritizing monitoring sites based on risk level of bullfrog presence and threat to native species. Though distribution models have been constructed for bullfrogs in the past, the previously constructed distribution models have focused on large regional to global scales (i.e. Ficetola et al. 2007(b), Ficetola et al. 2010, Giovanelli et al. 2008, Nori et al. 2011). The goal of this research was to construct a localized, water body- based distribution model for bullfrogs and prioritize wetlands for monitoring within the South Okanagan. I attempted to model habitat suitability under the changing landscape following habitat restorations, under recent historical climatic conditions, and under climate change predictions anticipating increased frequency and variability of drought and intensified precipitation periods (Cohen and Kulkarni 2001). Specifically, I aimed to: 1) estimate the distribution probability of bullfrogs previous to major wetland landscape changes beginning in 2004; and 2) project the historical bullfrog distribution onto the changed wetland landscape post 2004 to prioritize current wetland monitoring during average annual wetland conditions, consecutive flood years, and consecutive drought years.

Methods

Study area

I focused on the South Okanagan Basin Ecosection, within the South Okanagan Valley of British Columbia, Canada. The South Okanagan Valley runs primarily north to south. The valley is historically composed of rugged terrain at high elevations, open antelope-sagebrush grassland at mid to low elevations, and large lakes connected by the Okanagan River, wetland, and riparian habitat along the valley floor (Demarchi 2011). The region is classified as cold semi-arid according to Koppen climate classification, with annual precipitation levels of 319 mm and 38 % of the year experiencing daily maximum temperatures above 20 $^{\circ}$ C (ECCC 2013). The bullfrog distribution model extent was limited to where data for environmental predictor variables was known for modeled water bodies (Figure 2.1). The model focuses on all known ephemeral and permanent water bodies within a 233 km^2 area extending from Universal Trans Mercator coordinates 11U 312396 5466459 at the northwest corner, to 11U 324765 5430219 at the southeast corner, and ranges in elevation from 300 to 600 m above sea level.

The study area is a complex matrix of agriculture interspersed with residential and industrial areas, and patches of riparian and antelope/sagebrush grassland habitat. Three urban centers, Okanagan Falls, Oliver, and Osoyoos, supporting a total population of 19 000 people occur at the north border, middle, and south border of the study area (Our Okanagan 2016). In addition to extensive wetland loss and modification, over 77 % of the natural grassland habitat has been converted for urbanization or tree fruit, vineyard, and ground crop agriculture since the early 1900s (Lea 2008). The entire study area is connected by the channelized Okanagan River. The river channelization reduced river habitat by 93 % (Lea 2008) and resulted in multiple isolated, permanent water bodies staggered throughout the valley bottom, ranging in area from 0.05 ha to 10.6 ha. The Okanagan River also connects the study area from Vaseux Lake (278 ha) at the north end, to Osoyoos Lake (1480 ha) at the South end of the study area.

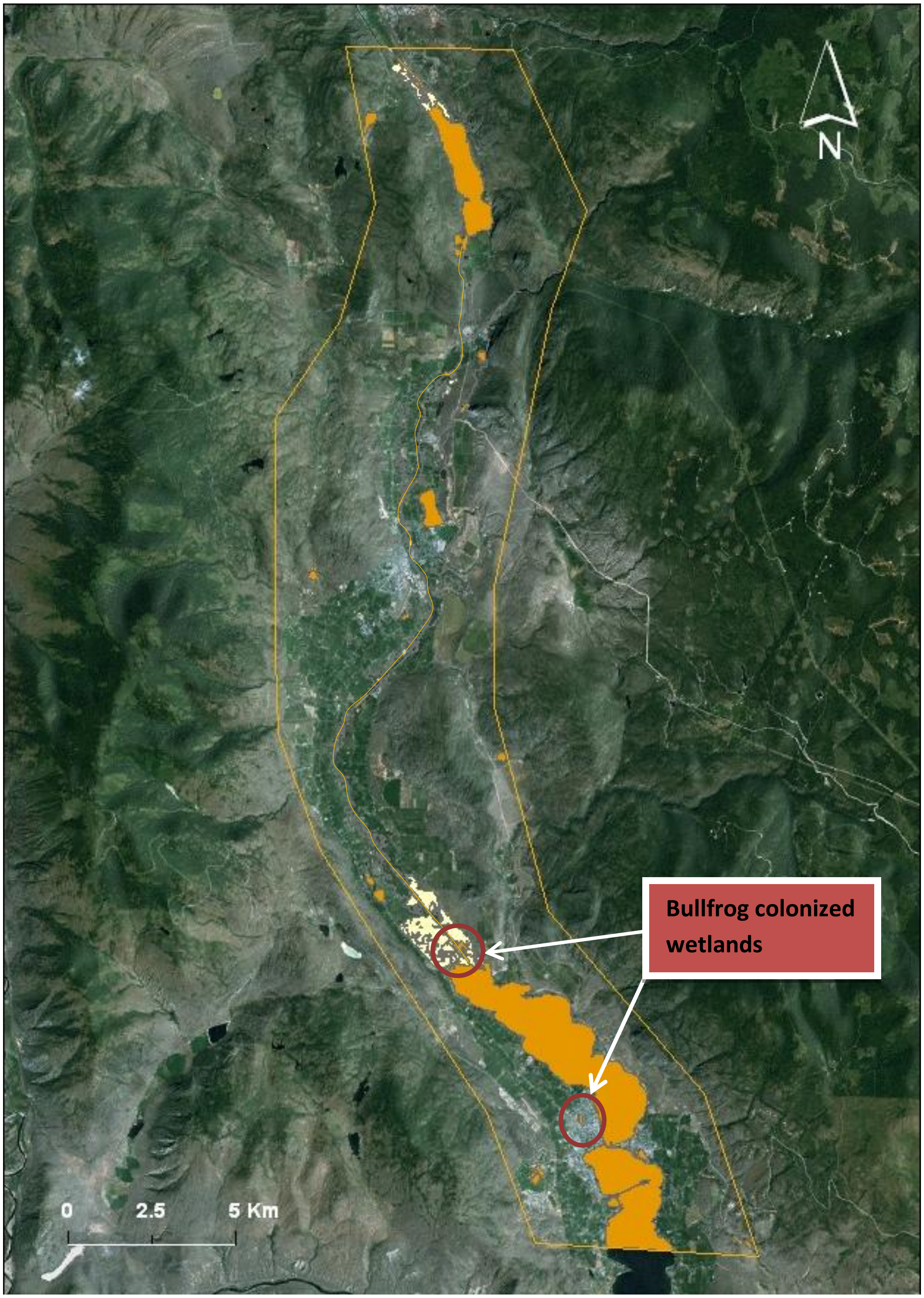


Figure 2.1 American bullfrog distribution model study area in the South Okanagan, British Columbia. All 235 known ephemeral and permanent water bodies between Okanagan Falls, Oliver, Osoyoos, and the USA border were modeled. Study area is denoted by orange lines; permanent water bodies are shaded dark orange; ephemeral water bodies are shaded cream. Map produced in ArcGIS 10.1 (2013).

Environmental predictor variables

The bullfrog habitat map created in this study attempts to distinguish suitability of individual water bodies within the study region. Data for bullfrog occurrence and environmental characteristics of each water body were obtained from herpetofauna monitoring within the South Okanagan (2003 through 2010; S. Ashpole et al., unpublished data), the Freshwater Wetlands spatial layer (DataBC 2012), WSA Water Feature layer from the BC Watershed Atlas (DataBC2012), Baseline Thematic Mapping Land Use Version 1- 1992 spatial layer (DataBC 2012), wetland enhancement spatial layers obtained from Ducks Unlimited Canada (2013), high resolution aerial imaging imported to ArcMap (Bing 2009), and location visits to ground-truth information. All presence and environmental predictor layers were projected to North American Datum 1983 Universal Trans Mercator Zone 11 North coordinate system and formatted at 10 m pixel resolution for Maxent using ArcGIS 10.1.

Seven environmental predictor variables were chosen based on factors previously illustrated to influence success or patterns of bullfrog dispersal and colonization, and the data available for all ponds modeled: hydroperiod (Cunningham et al. 2007, D'Amore et al. 2010, Shulse et al. 2010); water velocity (D'Amore et al. 2010, Fuller et al. 2011); surrounding matrix at 100 m, 500 m, and 1000 m distance from water bodies (Currie and Bellis 1969, D'Amore et al. 2010, Ingram and Raney 1943, Raney 1940); distance to known breeding location (Ingram and Raney 1943, Raney 1940), and presence of introduced predatory fish species (Adams et al. 2003, Cunningham et al. 2007, Werner and McPeek 1994, Shulse et al. 2010). Climatic data were excluded from the current study because of the relatively small scale of the study area and homogeneity of climate across the study area.

Distance to nearest breeding location was labeled continuous, while hydroperiod, water velocity, presence of introduced predatory fish, and surrounding matrix were labeled categorical. Hydroperiod was divided into permanent and ephemeral categories, with permanent ponds defined as water bodies holding water longer than 12 consecutive months, allowing for a full bullfrog reproduction cycle. Water velocity was categorized as stagnant, non-stagnant, or stagnant with considerable disruption, such as a large lake with consistent waves produced by heavy boat traffic or wind. Bullfrogs occasionally occur in small bays off of large lakes; bays within the two large lakes (> 278 ha) were included as separate polygons to capture potential predictor variable differences between the bays and lakes.

The surrounding matrix was included at three scales to capture the complex habitat matrix of the South Okanagan at various scales of previously recorded bullfrog movements (Ingram and Raney 1943, Raney 1940) to capture any potential scale related influences of surrounding matrix composition on bullfrog presence at water bodies. Each water body was assigned a surrounding matrix category at a 100 m, 500 m, and 1000 m buffer surrounding the water body. Buffer composition was assigned according to the majority class within each buffer, and determined using the Baseline Thematic Land Use spatial layer, aerial imaging, and buffer analysis in ArcGIS. Surrounding matrix was classified based on human modification, moisture retention, and cover characteristics. The surrounding matrix categories at 100 m were: high moisture/cover agriculture (i.e. tree fruit orchards); moderate moisture agriculture (i.e. irrigated hay and grazing fields); limited moisture/cover agriculture (i.e. vineyards); residential; industrial; high moisture/cover native riparian habitat (i.e. tree/shrub); moderate moisture/cover native riparian habitat (i.e. native riparian meadows); limited moisture/cover native habitat (i.e. antelope brush-sagebrush grasslands); and open water (i.e. lake). Surrounding matrix at 500 m and 1000 m were more broadly classified as agriculture, residential, native riparian, native desert, industrial, and open water (i.e. lakes).

Distribution modeling

Bullfrog distribution modeling was conducted using Maxent 3.3.3k (Philips et al. 2006; http://www.cs.princeton.edu/~schapire/maxent/). Maxent employs the ecological niche theory in conjunction with maximum entropy to predict bullfrog distribution based on presence-only data. Maxent is a machine-learning program which estimates the least biased distribution probability for a species, within an environmental predictor variables space, and within a geographic space (Elith et al. 2011, Phillips et al. 2006). Maxent assumes the most uniform probability distribution, under known constraints based on the environmental predictors, while assuming nothing that is unknown, and agreeing with everything that is known by researchers (Philips et al. 2006). The constraints are determined by averaging the value of each environmental variable across presence locations; predicted presence locations are expected to match the average values (Phillips et al. 2006). Maxent functions well at small scales, for invasive species distribution modeling, limited sample sizes, with categorical data, and has been shown to outperform other common species distribution modeling software and methods, including generalized linear modeling (GLM), generalized additive modeling (GAM), genetic algorithm for rule-set prediction (GARP), and bioclimatic niche modeling (BIOCLIM) (Elith et al. 2006, Franklin 2009, Navarro-Cerrillo et al. 2011, Pearson et al. 2007, Phillips et al. 2006). Although Maxent has proven to estimate species' probability distributions well, the model can be prone to over-fitting data, and care must be taken when extrapolating to locations outside the modeled study area (Phillips et al. 2006).

Three hundred and forty-two bullfrog presence records were partitioned into 72 % training (calibration) data and 28 % model testing (validation) data. Data partitioning was calculated according to Huberty's equation (Fielding and Bell 1997, Huberty 1994). Huberty's equation is designed to maximize the independent data set for model testing and minimize model prediction error (Huberty 1994), stating the training data to testing data ratio in predictive suitability modeling should be:

$$\frac{1}{1+\sqrt{p}-1},$$

where p is the number of environmental predictors included in the model. The model was run with 10-fold cross-validation and subsampling replication, with 10 000 background points randomly selected by Maxent (Philips and Dudik 2008). Boot-strapping replication was excluded because the presence sample size was large enough to accommodate partitioning presence data into groups without replacement. The regularization parameter was set at 1, determined by Phillips and Dudik (2008) to optimize model output. To assign probability of presence, Maxent uses model features, product, hinge, threshold, linear, quadratic, and categorical, to create a model function which minimizes the difference in environmental values between locations the species is found vs. where the species is not found (Elith et al. 2011, Phillips and Dudik 2008). The model features in this study were set at the default auto setting to allow the software's algorithms to optimize the model's function (Phillips and Dudik 2008).

Bullfrogs were intentionally introduced into the South Okanagan after extensive wetland habitat change was initiated in the early 1900s, and during the time the Okanagan River was channelized in the 1950s. In 2004, during the same time period in which bullfrog control was launched in the South Okanagan, more intensive wetland restoration and enhancement also started occurring throughout the valley. To capture the changes in wetland landscape, three model scenarios were run: 1) historical bullfrog distribution up to 2004; 2) historical bullfrog distribution projected onto current habitat conditions during typical conditions; 3) historical bullfrog distribution projected onto the current habitat conditions during consecutive drought years; and 4) current bullfrog distribution projected onto the current habitat conditions during consecutive flood years. The current habitat conditions were updated to include all constructed wetlands in the study area since 2004 and updated surrounding matrix categories where major habitat conservation land acquisitions occurred. For example, parcels of land historically farmed, but acquired for re-naturalization by conservation agencies were reclassified from agriculture to native habitat. Typical habitat conditions were simulated by retaining ephemeral wetlands and moisture-retaining habitat categories; drought years were simulated by excluding ephemeral water bodies from the model and re-categorizing moisture-retaining floodplains into dry land habitat except where irrigated habitat occurred; and flood years were simulated by reclassifying ephemeral wetlands as permanent (i.e. lasting long enough for one bullfrog reproductive cycle). Osoyoos Lake and the Okanagan River retained current boundaries during flood years, as these bodies are heavily anthropogenically developed along their margins and are managed for flood control.

Prior to projecting the historical habitat conditions onto the future map, the subsampled and cross-validated maps were compared to determine optimal parameters. Each model was evaluated using the Area Under the Receiver Operating Characteristic (ROC) Curve (AUC), and True Skill Statistic values (TSS) (Allouche et al. 2006). Typically, AUC values for species distribution measure a model's false positive versus true positive prediction rates (Fielding and

Bell 1997, Phillips et al. 2006). However, since Maxent only uses presence data, the AUC values are a measure of how well the model predicts presence locations vs. random background locations, represented as the fraction of the total study area predicted (Fielding and Bell 1997, Phillips et al. 2006). An AUC value of 0.5 means the model predicts presence locations no better than random, and an AUC value of 1 means the model predicts presence locations with perfect discrimination (Fielding and Bell 1997). Predictive distribution model evaluation using AUC is a common method; however, AUC accuracy for predictive distribution model evaluation is debated (Lobo et al. 2008). I evaluated the bullfrog model using TSS in conjunction with AUC to ensure a robust model evaluation. Similar to AUC, TSS is a measure of specificity and sensitivity. The TSS is not influenced by various model thresholds and provides for a more reliable measurement comparison (Allouche et al. 2006). Values of TSS range from -1 to +1, with values of -1 to 0 indicating model performance is no better than random (Allouche et al. 2006).

Importance of each environmental predictor variable in predicting bullfrog was determined using the jackknife and response curves generated by Maxent. Maxent estimates variable importance by jackknifing, or systematically running iterations leaving each predictor variable out in turn. The variable importance is expressed through the predictor variable’s contribution to improving the overall model, measured by how much the training gain, or closeness of fit of the model, changes when the focus variable is excluded (Phillips et al. 2006). When applied as an exponential, the gain gives the ratio of the average distribution probability for a presence pixel to the average probability of a background pixel (Phillips et al. 2006). Response curves are also determined by running model permutations excluding each predictor variable in turn (Phillips et al. 2006). The response curve for each predictor variable estimates the predicted probability of suitability for varying values of the predictor variables (Phillips et al. 2006).

After optimal parameters were determined, the historical bullfrog distribution conditions were projected onto the future habitat conditions to predict colonization patterns based on historical distribution. Each bullfrog distribution map was converted into a binary “suitable/unsuitable” map for model evaluation and further analysis in ArcGIS (Pearson 2008). Suitability was based on the minimum training presence threshold, meaning, map pixels with values occurring below the minimum environmental values used to train the model at presence locations were considered unsuitable. Minimum training presence threshold was selected because bullfrogs are an invasive species, and I want to minimize under-prediction of presence distribution (Pearson 2008). Following Maxent output import into ArcGIS, wetlands were prioritized for monitoring based on the combination of total amphibian species at risk presence and neighboring wetland density within 1000 m (Peterson et al. 2013, Semlitsch 2008) using reclassification and overlay tools. The value assigned to each water body represents a relative weight in monitoring priority. Number of neighboring wetlands was assumed to increase the likelihood of dispersing to or from the focus pond and promoting the species’ South Okanagan range expansion (Ingram and Raney

1943, Shulse et al. 2010, Youngquist and Bloom 2012). Amphibian species at risk presence was included to determine which ponds bullfrogs have the highest probability of co-occurring with, and negatively impacting, native species. The target species at risk included in prioritizing wetlands were the Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*), the Western Toad (*Anaxyrus boreas*), and the Great Basin Spadefoot (*Spea intermontana*).

Results

Two hundred and thirty five permanent and ephemeral wetlands were included in the South Okanagan introduced bullfrog distribution map. Before selecting the optimal bullfrog distribution map, the distribution model was run under cross-validation and subsampling replication methods to determine optimal sampling replicate method. Of the two methods, cross validation had a slightly higher, though significant TSS value (9.33 and 9.32, respectively; $p = 0.013$; Kruskal-Wallis test). The AUC values for each sampling method were similar, with subsampling having a slightly higher AUC value than cross-validation, with 0.998 ± 0.001 and 0.988 ± 0.007, respectively. The final historical distribution model was run using cross-validation and projected onto the future habitat scenarios based on the higher reliability of TSS scores for model evaluation (Allouche et al. 2006).

Historical bullfrog distribution

One hundred and twelve of the South Okanagan's wetlands previous to 2004 are deemed suitable for bullfrogs under a minimum training threshold of 0.024 without re-categorization for monitoring priority. The percent contribution to model performance, or influence of predictor variables on AUC values, was highest for surrounding matrix at 100 m, distance to breeding location, and water velocity in the historical distribution model (33.7 %, 26.7 %, and 21.7 %, respectively; Table 2.1). The lowest contributor to model performance was presence of introduced predatory fish (1.5 % contribution).

Table 2.1 Percent contribution of environmental predictor variables in the South Okanagan Valley Maxent bullfrog distribution model. Percent contribution represents the decrease in AUC values, normalized into percent values, when the respective predictor variable is omitted from analysis. Surrounding matrix at 100 m, water velocity, and distance to breeding location are most influential on predicted bullfrog distribution, while presence of introduced predatory fish is the least influential.

Predictor variable	**Percent contribution (%)**
Surrounding matrix at 100 m	33.7
Distance to breeding location	26.7
Water velocity	21.7
Surrounding matrix at 1000 m	7.2
Hydroperiod	6.6
Surrounding matrix at 500 m	2.6
Presence of introduced invasive fish	1.5

In addition to percent contribution to model performance, Maxent provides response curves describing the probability of habitat suitability within each predictor variable value or category (Table 2.2). Within surrounding matrix at 100 m, high moisture/high cover agriculture had a suitability probability of 75 %. All remaining matrix categories within 100 m, including residential areas, high-moisture/high cover native riparian, moderate moisture/moderate native riparian cover had suitability probabilities of < 5 %. Surrounding matrix at 500 m was 62.5 % for broad class agriculture, with all other matrix categories falling below 15 % at 500 m. Surrounding matrix at 1000 m had the highest suitability probabilities for broad-class agriculture at 53 %, followed by high moisture/high cover native riparian habitat at 34 %. Water bodies within 300 m of a known breeding location had suitability probabilities of 98 %; response to locations dropped to 10 % or lower beyond 300 m. Suitability of hydroperiod was 51 % for permanent and 33 % for ephemeral locations. Stagnant water velocity locations had suitability probability of 52.5 % (Table 2.2), and introduced fish presence and absences had suitability probabilities of 49.5 % and 44 %, respectively.

Table 2.2 Suitability probability responses to environmental predictor variables. Probabilities are calculated by systematically running permutations with each focus variable on its own.

Predictor variable	Predictor variable value/category	Suitability probability (%)
Land cover at 100 m	High moisture/cover agriculture	75
	Moderate moisture/cover native	21
	Moderate moisture/cover agriculture	8
	Limited moisture/cover agriculture	< 5
	Residential	< 6
	Industrial	< 7
	High moisture/cover native	< 8
	Limited moisture/cover native	< 9
	Open water	< 10
Land cover at 500 m	Agriculture - all	62.5
	Residential	15
	Industrial	1
	Native riparian	1
	Native desert/grassland	1
	Open water	1
Land cover at 1000 m	Agriculture - all	53
	Open water	34
	Native riparian	< 5
	Native desert/grassland	< 5
	Residential	< 1
	Industrial	< 1
Distance to breeding location	0 - 300 m	9
	> 300 m	< 5
Hydroperiod	Permanent	51
	Ephemeral	33
Water velocity	Stagnant	52.5
	Other	< 1
Presence of Invasive fish	Present	49.5
	Not detected	44

The environmental predictor variable with the highest jackknife training gain when used in isolation was distance to nearest breeding location (3.26), followed by surrounding matrix within a 100 m buffer of the water body (3.02). The lowest training gain of environmental predictor when run in isolation was that of introduced predatory fish presence (0.027). The test gain when distance to breeding habitat was excluded from the model decreased the overall model fit by 1.46. The second highest test gain when used in isolation was surrounding matrix at 100 m, though test gain did not decrease when land cover at 100 m was used in isolation. The lowest test gain was presence of introduced invasive fish.

Projecting future bullfrog distribution

Three model projections were run on wetland landscape changes post-2004 using the information obtained from the historical probability distribution model: estimated probability distribution under typical annual wetland conditions; estimated probability distribution under flood conditions; and estimated probability under drought conditions. The minimum training presence threshold used to determine suitability was 0.024, with the fractional predicted area 0.737 ($p < 0.05$). Cells with environmental value scores less than 0.024 were deemed unsuitable bullfrog habitat.

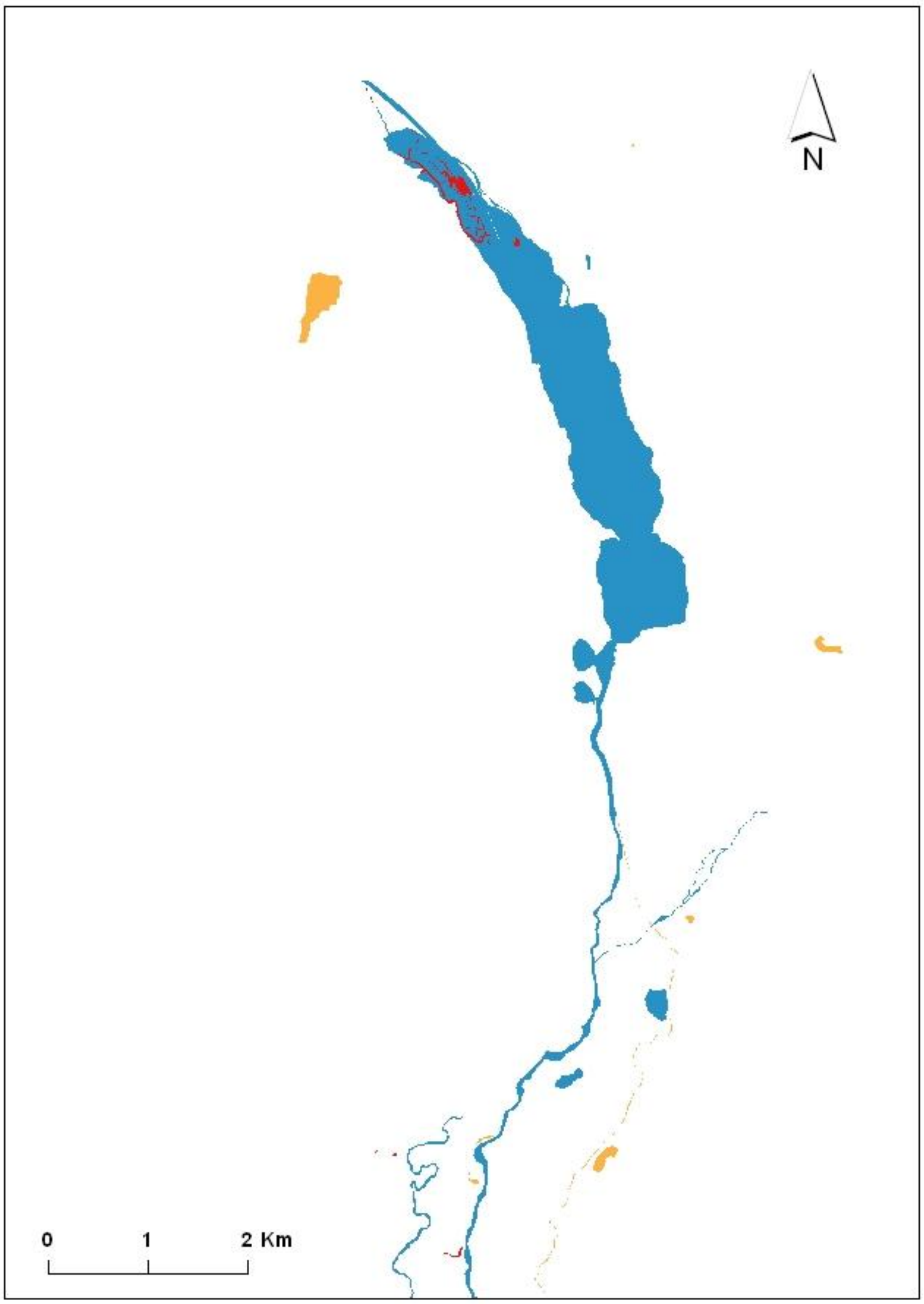
Following relative, ranked monitoring prioritization based on species at risk presence and number of surrounding wetlands within 1000 m, the number of ranked priority wetland sites for monitoring varied between scenarios (Table 2.3; Figures 2.2 – 2.4). During typical wetland conditions, with ephemeral water bodies lasting shorter than 12 consecutive months, 60.5 % of the South Okanagan's water bodies are weighted over 0.50 for monitoring priority. Flood conditions increased the proportion of priority ponds to 71 %, and drought conditions decreased the proportion to 47. In all scenarios, suitability is highest stagnant, permanent wetlands surrounded by high cover/moisture agriculture. Ephemeral ponds are also weighted heavily in areas, particularly along the Okanagan River Channel where higher wetland density occurs. These rankings consider bullfrog colonization through natural dispersal facilitated by higher surrounding wetland density, and do not account for human-facilitated placements of bullfrogs into water bodies. Note also that the values do not represent an absolute value for suitability or presence, but rather denote a relative likelihood of bullfrog presence for water bodies in relation to each other.

Table 2.3 Percentage of wetlands in ranked priority categories for bullfrog monitoring at wetlands in the South Okanagan. Following Maxent distribution estimation, each water body was reclassified according to amphibian species at risk present and number of neighbor wetlands within 1000 m. Unsuitable habitat occurs at rank values below 0.35.

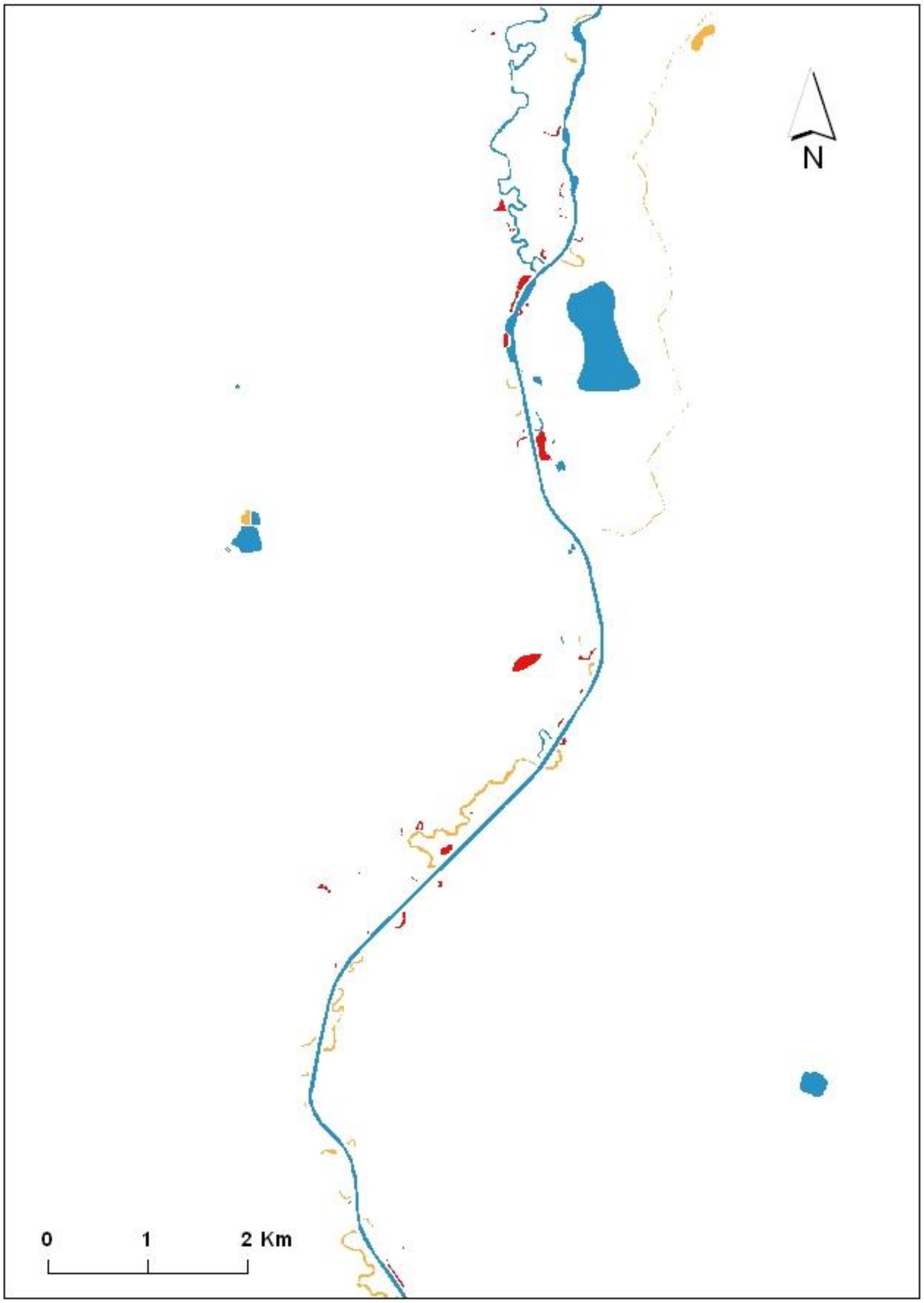
Scenario	Monitoring priority rank unsuitable (< 0.35) (%)	Monitoring priority rank 0.35 – 0.50 (%)	Monitoring priority rank > 0.50 (%)
Average conditions	25	14.5	60.5
Flood conditions	13.2	15.3	71.5
Drought conditions	37	16	47

Figure 2.2 Ranked, relative water body priority for introduced bullfrog monitoring in the South Okanagan during average conditions with ephemeral ponds holding surface water less than 12 consecutive months. Monitoring priority is based on probability of suitability output from Maxent, with water bodies ranked based on presence of amphibian species at risk and number of neighboring wetlands. The map has been divided to allow for closer viewing. A) Depicts the north section of the study area; B) depicts the mid-section of the study area; and C) depicts the south section of the study area. Warm colors represent higher relative priority monitoring rank. Note: monitoring priority values are relative weights assigned within each scenario; maps cannot be directly compared across scenarios. Monitoring priority is viewed with wetlands in relation to each other for each scenario.

A)



B)



C)

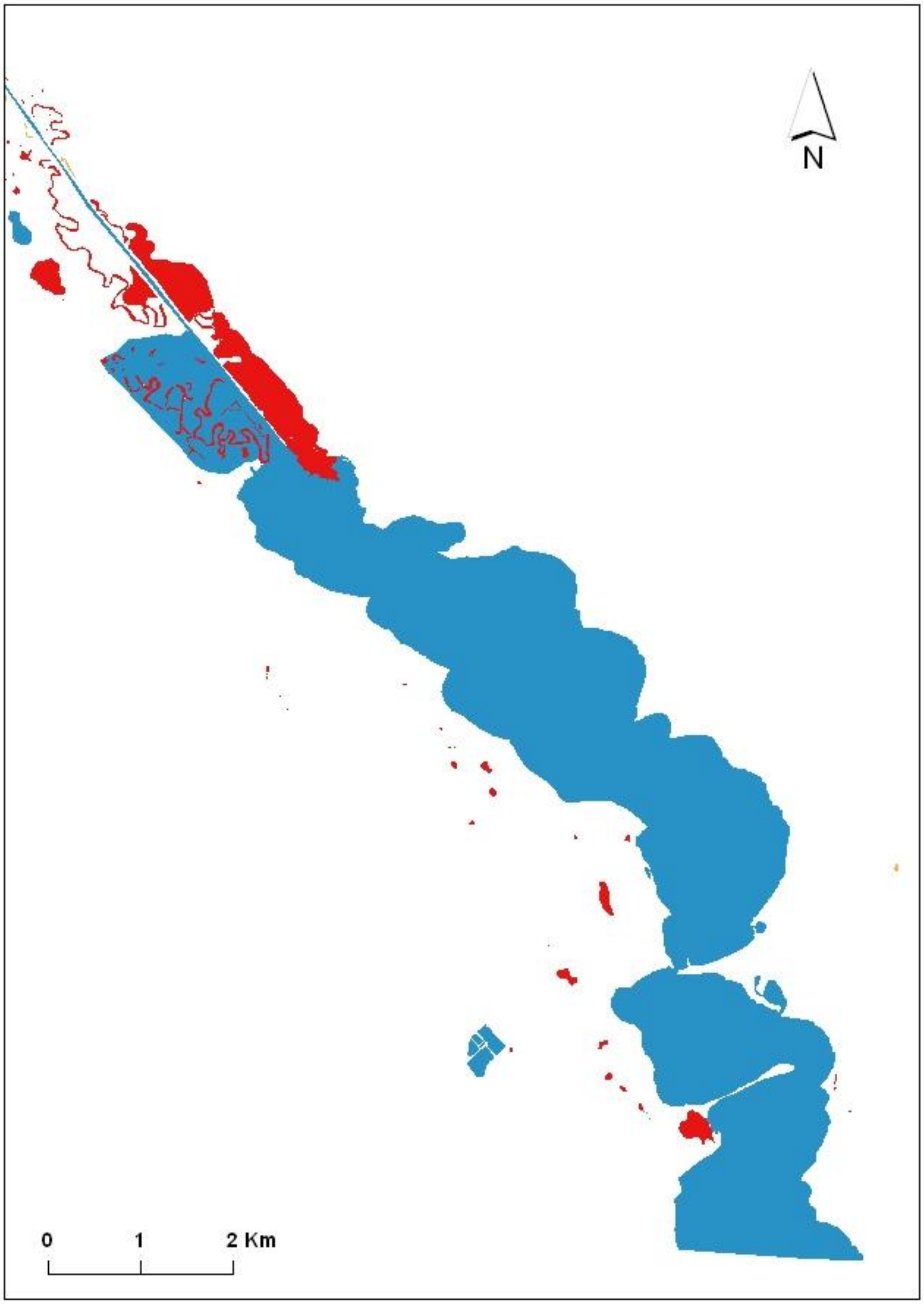
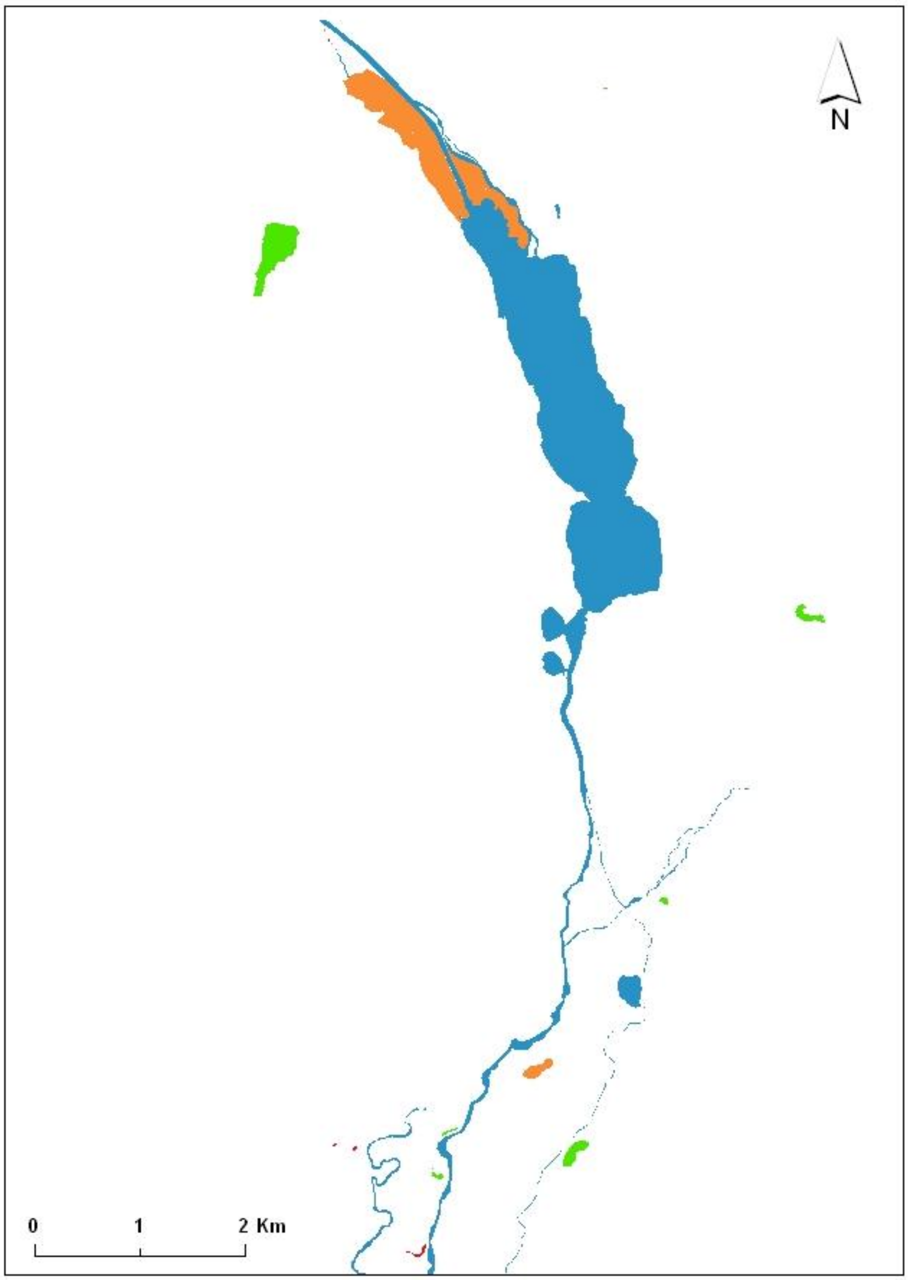
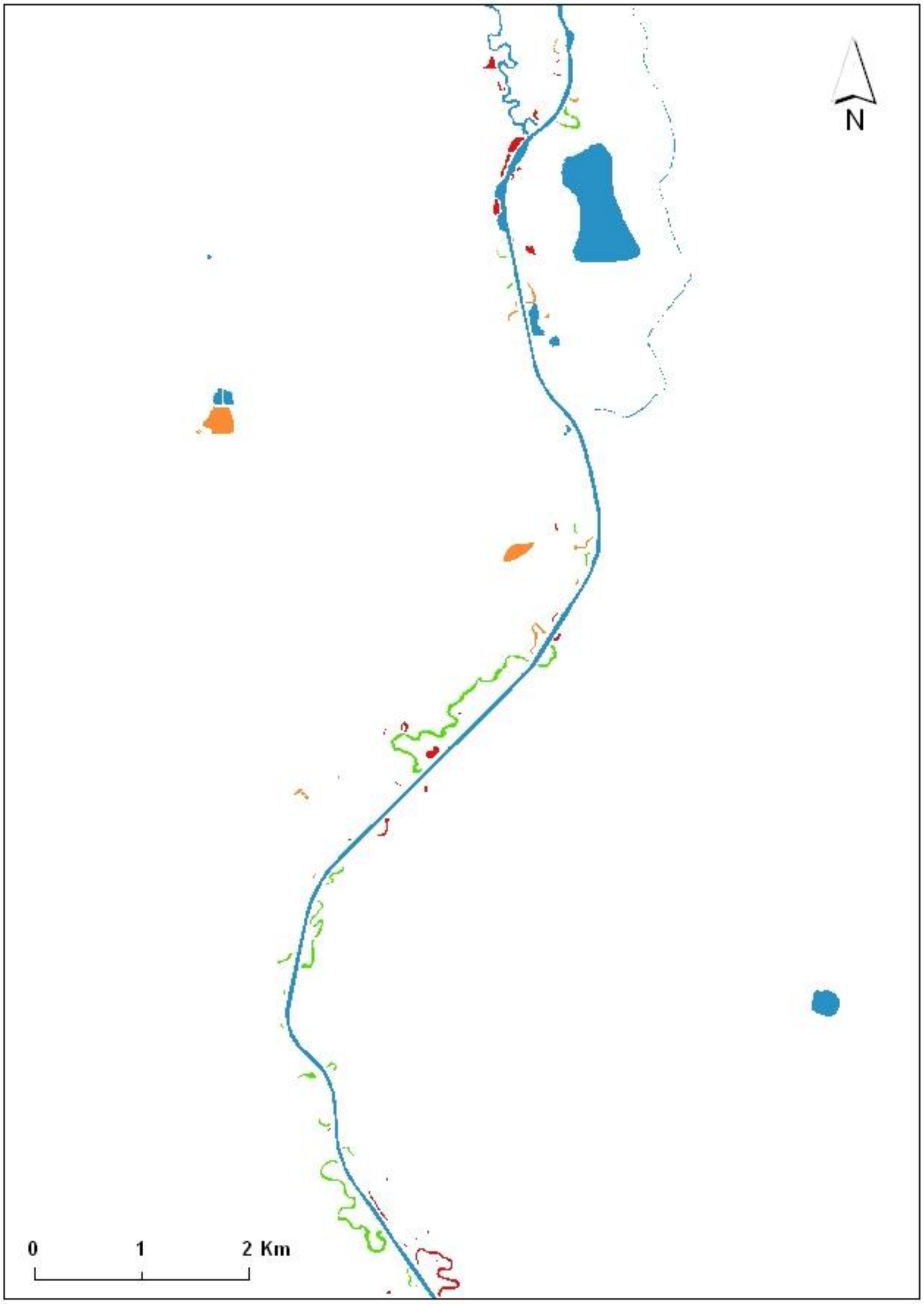


Figure 2.3 Ranked, relative water body priority for introduced bullfrog monitoring in the South Okanagan during flood conditions with ephemeral ponds holding surface water longer than 12 consecutive months. Monitoring priority is based on probability of suitability output from Maxent, with water bodies ranked based on presence of amphibian species at risk and number of neighboring wetlands. The map has been divided to allow for closer viewing. A) Depicts the north section of the study area; B) depicts the mid-section of the study area; and C) depicts the south section of the study area. Warm colors represent higher relative priority monitoring rank. Note: monitoring priority values are relative weights assigned within each scenario; maps cannot be directly compared across scenarios. Monitoring priority is viewed with wetlands in relation to each other for each scenario.

A)



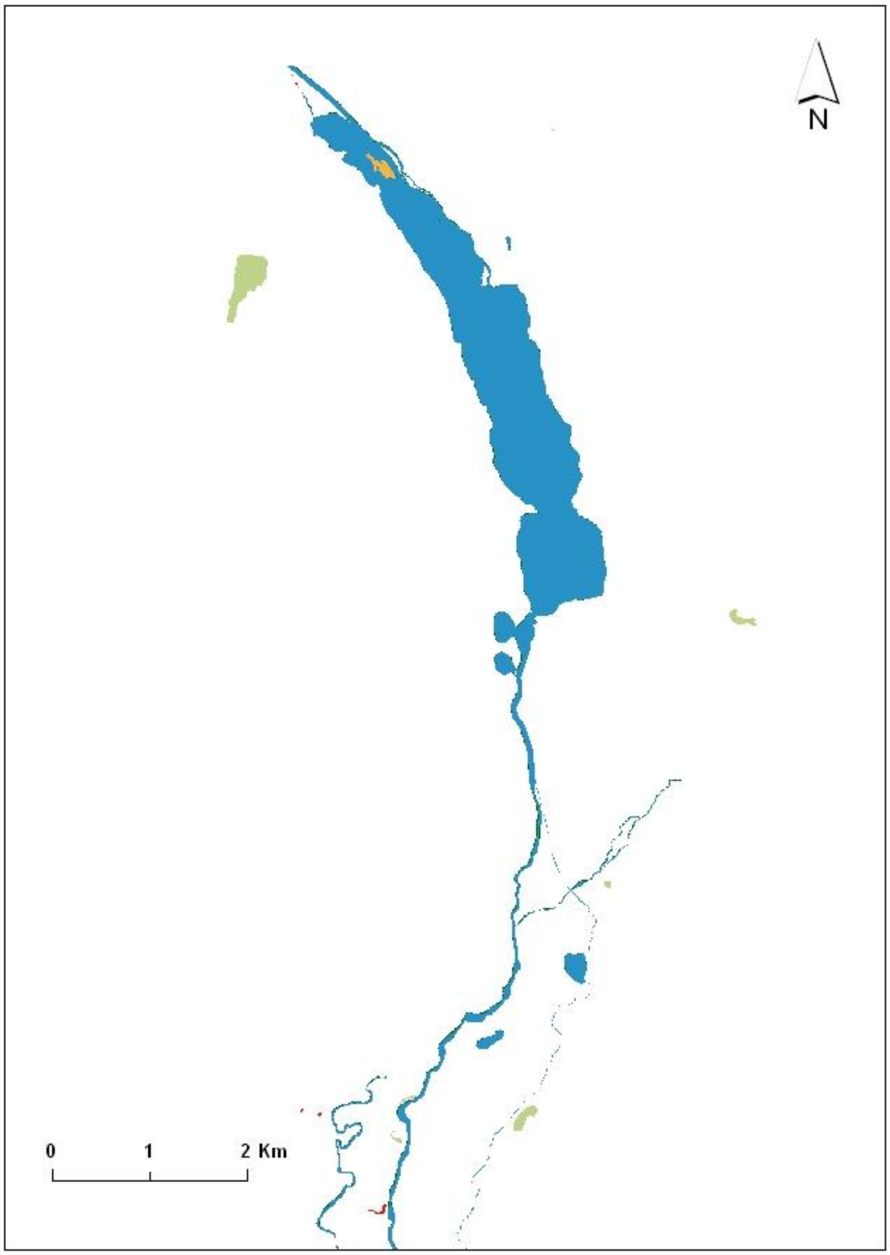
B)



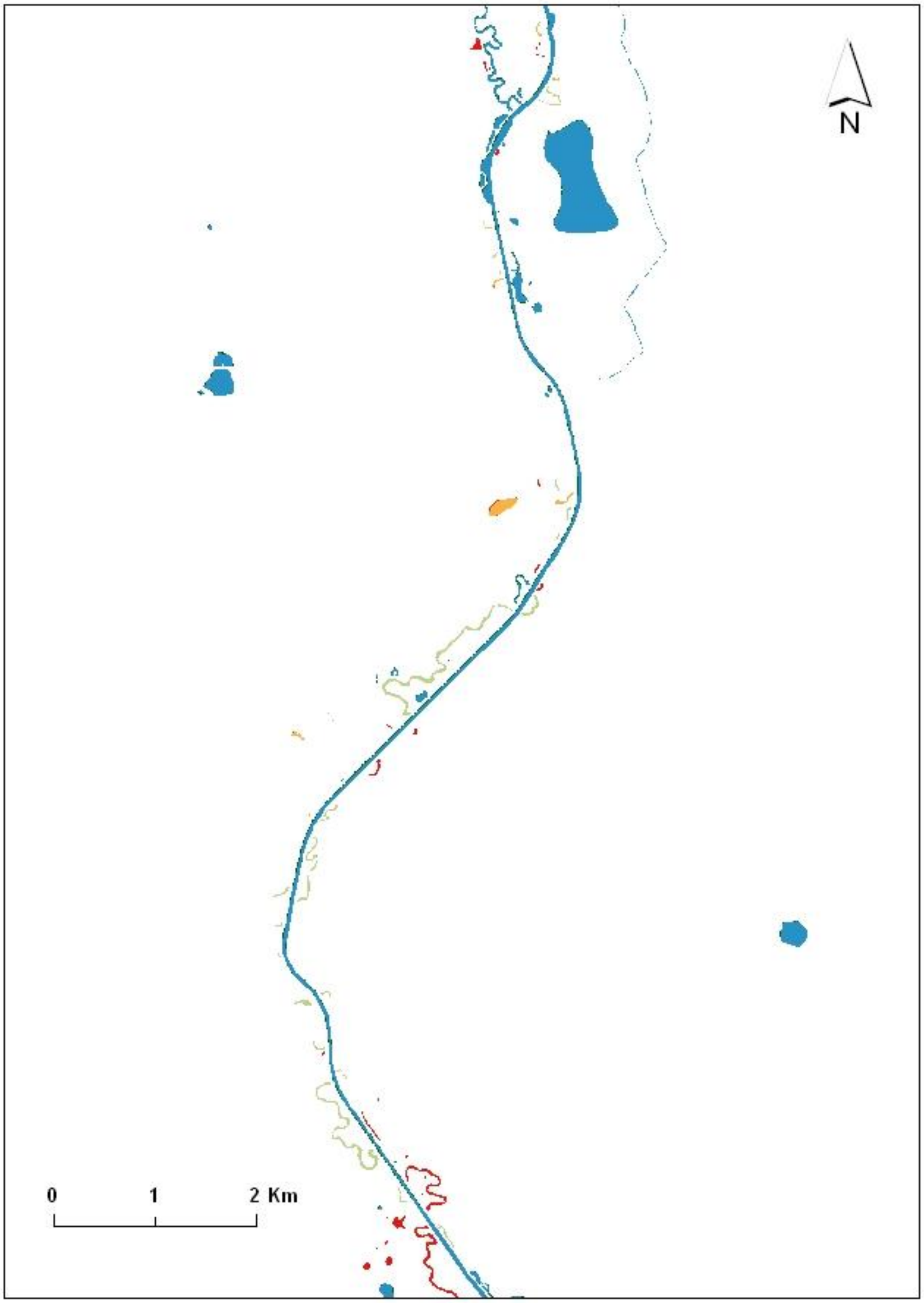
C)

Figure 2.4 Ranked, relative water body priority for introduced bullfrog monitoring in the South Okanagan during drought conditions with ephemeral ponds excluded and surrounding matrix increased to the next lower moisture category, except where irrigated habitat exists. Monitoring priority is based on probability of suitability output from Maxent, with water bodies ranked based on presence of amphibian species at risk and number of neighboring wetlands. The map has been divided to allow for closer viewing. A) Depicts the north section of the study area; B) depicts the central of the study area; and C) depicts the south section of the study area. Warm colors represent higher relative priority monitoring rank. Note: monitoring priority values are relative weights assigned within each scenario; maps cannot be directly compared across scenarios. Monitoring priority is viewed with wetlands in relation to each other for each scenario.

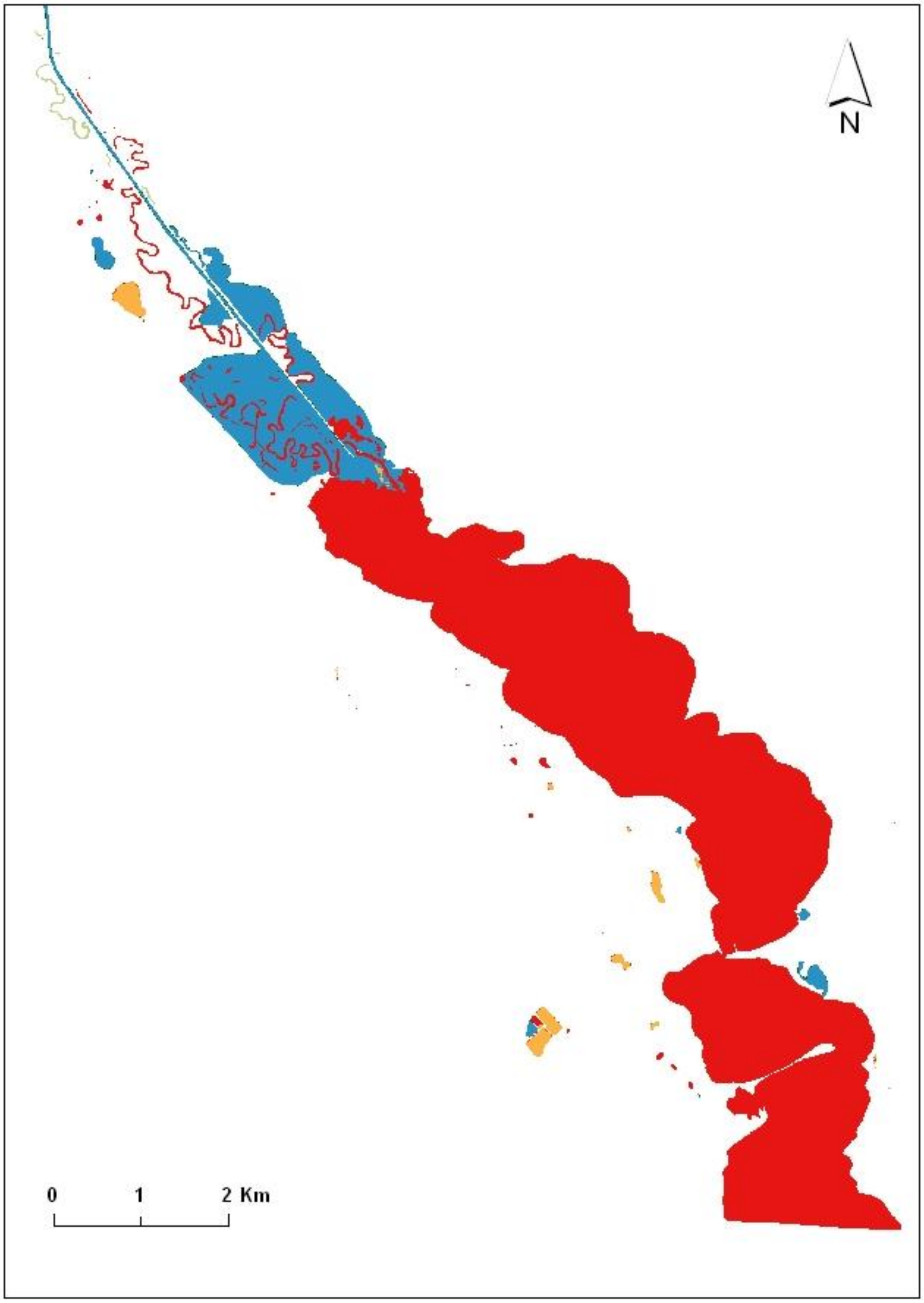
A)



B)



C)



Discussion

The goal of this research was to develop a predictive bullfrog distribution model for the South Okanagan to aid decision-making for future monitoring in the face of reduced bullfrog densities following control efforts, reduced financial resources available for bullfrog control, a changed wetland landscape following increased regional habitat restoration efforts, and increasing, variable weather conditions predicted by regional climate change models. I modeled the historical distribution of bullfrogs to determine habitat suitability conditions within the South Okanagan, then projected the historical distribution onto the changed wetland landscape post 2004 during average annual weather conditions, sustained flood conditions, and sustained drought conditions. The predicted suitable wetlands were then ranked for monitoring priority according to surrounding wetland density and presence of species at risk.

Historical bullfrog distribution

Bullfrog probability of presence in the South Okanagan is highest for wetlands occurring in permanent, stagnant, ponds within 300 m of a historic breeding location, surrounded within 100 m by high moisture/cover agricultural land such as tree fruit orchards. The South Okanagan climate is very hot and arid, with native habitat dominated by dry, open grasslands and ephemeral ponds at low elevations. The tree fruit agricultural landscape within the South Okanagan provides more cover, higher ground moisture levels, and is more likely to contain stagnant, permanent irrigation ponds required for successful bullfrog breeding. The presence of bullfrogs in high moisture areas in the South Okanagan may be due to the bullfrogs' large body size which increases desiccation rates and results in the bullfrogs' tendency to use moisture-retaining habitat (Willis et al. 1956, Youngquist and Boone 2012). Our results are also consistent with other studies which have found bullfrog invasion to occur in human modified, stagnant, permanent water bodies in agricultural landscapes (Bunnell and Zampella 2008, D'Amore et al. 2010).

Distance to the nearest breeding location was also a strong contributor to bullfrog distribution probability in the South Okanagan. Typically, species distribution models use only breeding presence records whenever possible to ensure habitat which may be unsuitable but temporarily housing the species is not included in the distribution model. The South Okanagan bullfrog range includes ponds consistently observed with multiple individuals but no signs of successful reproduction. The non-breeding ponds were included to ensure wetlands that may facilitate dispersal are also included to improve the chance of successfully removing all individuals from the South Okanagan. However, the decrease in training gain from the jackknife tests when breeding location distance was excluded from permutations indicates that the breeding location variable contains information not captured by other variables. Water temperature and chemistry profiles, distance from shoreline to 1 m depth, and substrate composition influence bullfrog presence in ponds (Graves and Anderson 1987). The scope of this study and need for every modeled water body to have known environmental variable values precluded the inclusion of more complex descriptors of wetlands such as the temperature profiles and shore distance to 1 m depth. Further research into these pond characteristics will help determine the intricate differences between the breeding and non-breeding locations. Regardless, the results of the historical distribution model indicate that monitoring efforts should focus on wetlands clustered within 300 m around bullfrog breeding locations.

Though our model was consistent with other studies indicating bullfrog invasion is more likely to occur in agricultural environments, our results differed from other studies with respect to moderate cover and moisture-retaining areas, such as such as golf courses, crop fields, and ground crop agriculture (Boone et al. 2008). In other regions, bullfrogs occur in ground crop landscapes, golf courses, and have been observed dispersing through dry, harrowed hay fields (Boone et al. 2008, Willis et al. 1956). The discrepancy between the results in the South Okanagan and previous studies may be due to the extremely hot, dry, climate during the active breeding and dispersal period of bullfrogs. The dry climate combined with landscape that offers less protection from desiccation may impede bullfrog movement through areas such as hay fields. Bullfrogs occurring in similar hot, dry climates surrounded by hot, arid landscapes have shown dispersal patterns more consistent with human facilitation than natural dispersal (Luja and Rodriguez-Estrella 2011). Although the current model indicates wetlands surrounded by ground crop and golf courses are less likely to contain bullfrog populations, these sites should not be entirely excluded from future monitoring given the possibility for human-facilitated introductions.

Apart from the hot, dry South Okanagan climate potentially preventing bullfrogs from successfully colonizing open field and ground crop wetlands, pond conditions related to tree cover may also factor in to the absence of bullfrogs in open cover ponds. In addition to tree fruit agricultural areas, bullfrogs are also found in oxbows with high shoreline tree cover within the South Okanagan. Bullfrogs are correlated with woody debris and leaf litter in wetlands in regions outside of the South Okanagan (Lichtenberg et al. 2006). The present bullfrog model did not account for specific habitat complexity measures such as shoreline vegetation, leaf litter, and woody debris composition. Future comparisons of habitat structure and composition complexity, temperature profiles, and water quality between sites, not examined in the present study, may help explain the difference in bullfrog occurrence between open wetlands and the more covered oxbows in the South Okanagan.

The current South Okanagan bullfrog distribution model also differed from other bullfrog habitat studies with respect to introduced predatory fish presence (Adams et al. 2003, Bunnell and Zampella 2008, Cunningham et al. 2007). Despite research indicating bullfrog population establishment is facilitated by introduced predatory fish (Adams et al. 2003, Bunnell and Zampella 2008, Cunningham et al. 2007), presence of introduced predatory fish was not a strong contributor to probability of bullfrog presence in the South Okanagan. The model results in the present study may have been confounded by the high occurrence of introduced fish throughout

South Okanagan water bodies regardless of bullfrog presence. The model in the current study also did not discriminate between the species of introduced fish present or density of fish, which may be important when considering the interactions between bullfrog population establishment and fish presence.

Under the minimum training presence threshold applied in the present South Okanagan historical bullfrog distribution model, 48 % of wetlands were deemed suitable for bullfrog presence prior to wetland landscape changes in 2004. Expanded wetland monitoring conducted throughout the region during the bullfrog control period suggests this estimate over-predicts actual presence of bullfrogs within the South Okanagan. However, monitoring was more intense at ponds with known bullfrog presence and some populations may remain undetected in other wetlands. The South Okanagan climate is also very hot and dry, and may have played a larger role in restricting bullfrog dispersal than the predictor variables applied to the present model. Although I attempted to captured dispersal conditions related to habitat indirectly through surrounding matrix composition at varying scales and wetland density within 1000 m (Currie and Bellis 1969, D'Amore et al. 2010, Ingram and Raney 1943, Peterson et al. 2013), dispersal constraints were not directly measured which may also have decreased the model's accuracy (Vaclavik and Meentemeyer 2009). Although the minimum presence threshold likely over predicts some suitable habitat in the South Okanagan, the present model highlights water bodies that should be given more monitoring attention. Given the goal of complete population suppression in the South Okanagan, a conservative approach to predicting distribution may help prevent overlooking potential presence areas (Pearson 2008).

The pre-2004 historical bullfrog distribution estimation map had an AUC of 0.9975 ± 0.0011, and a TSS score of 0.933. Although the model does not contain intricate relationship details, such as water quality or temperature among sites, and may not capture variables specific to breeding success, the model scores indicate the model has predictive capacities within the study area, and can be used to approximate projected changes in the following future landscape scenarios in conjunction with ongoing monitoring. Although the model scores indicate a fair level of confidence, this model may be confounded by the high abundances at a limited number of overall presence locations within the valley, relative to the total number of available wetlands. Additional monitoring is still recommended to compliment these results.

Projecting future bullfrog distribution

Introduced species are most efficiently controlled before population establishment occurs. Since control efforts began in 2004, the South Okanagan bullfrog control program has reduced detections of introduced bullfrogs in 2011 and 2012 to 0 observations of all life stages (Lukey et al. 2012). The next phase in bullfrog control is the development of appropriate methods to assist decision-making regarding monitoring resource allocation to prevent the re-establishment of potentially remaining undetected individuals, or new introductions. The goals of this paper were to model wetlands within the South Okanagan, and prioritize the wetlands for monitoring. The preceding historical distribution estimation map was projected onto the post-2004 landscape with the newly restored or enhanced ponds to determine which water bodies should be considered monitoring priority.

A minimum training presence threshold of 0.024, the lowest cumulative value of environmental predictor variables associated with presence sites, was used to delineate suitable and not suitable habitat. Each wetland was then ranked for priority based on presence of provincially endangered or threatened amphibian species and number of neighboring wetlands within 1000 m. The additional ranking of ponds was necessary in ensuring wetlands are monitored as efficiently as possible given the extremely limited management resources available. The resulting output is an individual-based list of wetlands and the relative priority that should be placed for monitoring each. The priority wetlands are primarily permanent, stagnant tree fruit or other high moisture/cover agricultural sites. The percentage of wetlands ranked high priority varied with flood and drought conditions, with the proportion of wetlands for priority monitoring ranked over 0.5 ranging from 71 % in flood conditions, to 47 % in the drought conditions. All scenarios resulted in relatively high numbers of ponds estimated as potential distribution sites; however, minimizing the likelihood of under predicting potential habitat is crucial in maintaining the success of the bullfrog control program. The comprehensive list of rankings should also be regarded with some care, as environmental variables inappropriate for bullfrogs likely exist that were not captured in the distribution estimation. For example, some water bodies labeled priority in the study site are saline, and potentially outside of the range of bullfrog environmental tolerances (Brown and Walls 2013). The model did not include detail related to pond salinity or other water chemistry which may influence bullfrog presence.

All scenarios resulted in some ephemeral water bodies listed as higher relative monitoring priority despite a probability of suitability for ephemeral water bodies being lower than permanent. The relatively high level of monitoring priority rank for ephemeral ponds is likely due to the clustered nature of ephemeral ponds along floodplains, and the requirement of all the target species at risk requiring, and therefore occurring, at high frequencies in ephemeral ponds. Although bullfrogs prefer permanent water bodies, bullfrogs use ephemeral water bodies for dispersal and summer foraging (Cunningham et al. 2007, Gahl et al. 2009). Bullfrogs can also reproduce in one breeding season in northern parts of the central USA and regions with warm climates (Provenzano and Boone 2009). Bullfrogs on Vancouver Island, BC, are capable of faster transformation, transforming from egg to juvenile within 14 months (Govindarajulu et al. 2006). Although 14 months is longer than the classified 12 month ephemeral pond length in the present study, increased hydroperiod of ephemeral ponds may be facilitated by the increased precipitation projected by Okanagan regional climate change models (Cohen and Kulkarni 2001). Bullfrogs using ephemeral ponds for any purpose have the opportunity to encounter all three of the native South Okanagan amphibian species which are provincially endangered and threatened. Of particular concern are the Blotched Tiger Salamanders who share similar breeding habitat needs as bullfrogs. Although Tiger salamanders prey on bullfrog larvae (McIntyre and McCollum 2000), the low density of remaining Tiger Salamander populations in South Okanagan may not be robust enough to counter additional predatory pressure of bullfrogs on the salamander populations. Maintaining monitoring attention on ephemeral ponds is important in ensuring native species are sheltered from potential negative effects of introduced bullfrogs.

Although variations exist among prioritizations, the priority monitoring sites in all scenarios are concentrated along the Okanagan Channel, within the valley bottom, and closer to an urban center, where the core breeding populations were detected. Both areas have high concentrations of privately owned land (South Okanagan Similkameen Conservation Program 2000). Monitoring bullfrog populations on private land presents many challenges, including permission to access sites in the long-run. Monitoring efforts need to continue to maintain focus on involving landowners in monitoring and reporting, and providing continual education to landowners living around high-risk properties. Citizen science is a useful tool for conservation, particularly if the goal is to obtain as many observances of a species as possible, or when dealing with invasive species (Dickinson et al. 2012, Crall et al. 2010). However, tadpoles and adults of native South Okanagan species including the Columbia Spotted Frog (*Rana luteiventris*) have been mistaken by resource managers with moderate levels of bullfrog identification training in the past (S. Ashpole pers. comm.). South Okanagan education needs to maintain a strict observe and report message to reduce misidentification and negative impacts on native amphibians should land owners or other citizens decide to get involved in control (S. Ashpole, pers. comm., Andreu et al. 2009, Somaweera et al. 2010).

The priority areas also occur where multiple wetland restoration efforts are under way, within the valley floodplain and low-lying riparian areas along the Okanagan Channel. These restoration efforts ultimately increase the landscape connectivity for bullfrogs by increasing the quantity of wetted areas available and decreasing distance between water bodies. Awareness among restoration professionals to monitor pond restoration for bullfrogs is critical to ensuring restoration efforts do not inadvertently increase the dispersal and reproduction of bullfrogs. A key example is the wetland restoration immediately adjacent to the SOWMA bullfrog locations; multiple oxbows have been excavated and restored following decades of infilling, creating permanent water bodies with potential for ideal colonization conditions from the immediately adjacent bullfrog locations.

The priority monitoring assumptions and wetland locations in this study operate on the assumption that bullfrogs are naturally dispersing. However, bullfrogs are a highly human-facilitated species, and introductions to wetlands can occur wherever humans have access to. Despite being a widely regarded invasive species, people continue to intentionally transport bullfrogs throughout the world for multiple reasons (Luja and Rodriguez-Estrella 2011).

Additional models can be run excluding any distance variables to determine potential habitat outside of bullfrog dispersal patterns in the South Okanagan. Models can also be run experimenting with various source populations and selecting clusters of wetlands around the experimental source populations.

The current predictive distribution model in this study provides a wetland-specific ranked list to aid bullfrog monitoring decisions. Although the current distribution model holds predictive power for estimating bullfrog distribution probability in the South Okanagan, the model was restricted to known data for all water bodies included in the model. Specific parameters, such as vegetation structure, depth, and water temperature and chemical profiles, which may influence bullfrog presence (Fuller et al. 2011, Graves and Anderson 1987), were not captured in the study. Including such predictor variables in future modeling will strengthen the predictive power of the model. The South Okanagan landscape is also rapidly changing, with urban development expanding (Pidwirny et al. 2002), agricultural land use largely being converted from high moisture, high cover tree fruit orchards, to low cover, dry open vineyards (Hira and Bwenge 2011), and continued wetland enhancement and restorations (Ashpole 2015).

Although the present bullfrog distributions projections likely over-predict historical and potential future distributions in the South Okanagan, the present model will aid decision-making by providing wetland criteria for which to focus surveys on: stagnant, permanent wetlands surrounded within 100 m by high moisture retaining agriculture and within 300 m of breeding ponds. The present bullfrog distribution projections also prioritize water bodies based on species at risk presence, and highlight key areas requiring monitoring effort. The present model was also structured and constructed with the intent that environmental predictor updates and projection reiterations can be easily conducted should additional wetland and land use data become available.

Chapter 3. Introduced American bullfrog (*Lithobates catesbeianus* Shaw 1802) detection and removal effort in the South Okanagan, British Columbia (2004 to 2012)

Overview

Introduced bullfrogs are associated with extensive negative impacts on native wildlife populations, particularly native amphibians. Bullfrogs were detected in the South Okanagan, British Columbia, in 2003. The South Okanagan is home to a unique species assemblage within Canada. One half of the native amphibian species present are federally threatened, endangered, or of special concern. Existing threats to native amphibian populations, combined with the limited overall detected locations, isolated nature of the colonized ponds, and wide body of literature suggesting bullfrogs negatively impact native wildlife, prompted conservation managers to prioritize bullfrog removal in the South Okanagan. An on-going bullfrog control program was initiated in 2004 in a multi-agency collaborative effort. The goal of this study was to: 1) describe the methods, total effort, and results of the bullfrog management; and 2) highlight key management lessons learnt through bullfrog control in the South Okanagan. Nine years of introduced bullfrog detection and removal effort resulted in 11 102 introduced individual bullfrogs and egg masses detected and removed at 7 of the 125 surveyed sites in the South Okanagan between 2005 and 2012. Of particular note are zero bullfrog detections of all life stages which occurred in the final two years of monitoring, 2011 and 2012. Main detection and removal effort included auditory surveys, active searches, Gee trapping, and night-time canoe searches. Approximately 640 and 850 total search hours were expended for auditory and active searches respectively, and 24 670 total 24-hour trap day equivalents of Gee trapping. An additional 310 hours were spent on night-time canoe searches, 2 940 hours were spent on automated auditory recording, and 65 hours on seine netting and night-time active searches by foot. Ninety trap day equivalents were spent on basking trapping. The catch per unit effort (CPUE) of the main methods varied widely among methods and sites, from 0 to 16 ± 55 individuals per trap day for Gee trapping, to 0 to 41 ± 46 individuals per search hour for active searches, and 0 to 28 individuals per hour for canoe searches. The results indicate that the combination of methods selected was successful in reducing abundance at the colonized ponds. However, the variation in CPUE for each method supports the premise that effort needs to be maintained for detection and removal in subsequent years as there are likely additional individuals at low enough densities to avoid detection by standard methods. Monitoring into the future to ensure suppression is recommended for minimum 10 years. Major lessons learned include: each water body requires an adaptive and robust approach; removal efforts must be persistent; future monitoring should focus on a slight increase in visual effort and slight reduction in auditory effort when populations are at low abundances; and repetitive training is required for observers to ensure accurate identification. The future of bullfrog control in the South Okanagan presents challenges under low population abundance and low detectability, and reduced funding while population suppression is at a critical point in preventing re-establishment. Multiple collaborative efforts combining different agency goals and target species is recommended to help alleviate the resource-limiting pressure for monitoring.

Introduction

Aquatic introduced invasive species are an ongoing concern in Canada, with an estimated establishment rate of 15 species per decade (Department of Fisheries and Oceans Canada (DFO) 2004). Globally invasive American bullfrogs, *Lithobates catesbeiana*, are of particular concern in western Canada. Bullfrogs are native to Eastern North America, but have been transplanted and become established outside of their native range.

Figure 3. 1 Global distribution of American bullfrogs. Yellow region indicates native range; red circles indicate introduced populations; black circles indicate introduced British Columbia populations. Introduced bullfrog populations have been recorded on all continents except Antarctica, Africa, and Australia (Global Invasive Species Database 2005). World map adapted from Wikimedia Commons (2011) and distribution data obtained from the Global Invasive Species Database (2005).

Introduced bullfrog invasions are not associated with extensive economic costs related to infrastructure damage or water quality issues as with other introduced aquatic species (Stitt et al. 2009). However, introduced bullfrogs are associated with extensive negative impacts on native wildlife populations, particularly native amphibians. Introduced bullfrogs outcompete (Kiesecker et al. 2001, Kupferberg 1997, Wu et al. 2005), predate upon (Kiesecker and Blaustein 1997, Wu et al. 2005), transmit disease to (Garner et al. 2006, Mazzoni et al. 2009, Schloegel et al. 2012), interfere with reproductive activity of (D'Amore et al. 2009, Pearl et al. 2005), and act in synergy with introduced predatory fish and chemical pollutants to amplify survival pressure on native amphibians (Adams et al. 2003, Boone et al. 2007, Maret et al. 2006).

Bullfrogs were detected by biologists and conservation managers in the South Okanagan, British Columbia, in 2003 (S. Ashpole, pers. comm.). The bullfrogs were initially introduced into the

South Okanagan into one agricultural pond in the 1950s by a local farmer, though the import source and number of introduced individuals is unknown (K. Favrholdt pers. comm.). The purpose of the initial bullfrog introduction was food production, but this goal was abandoned for unknown reasons and the introduced individuals left unmanaged. The detection of introduced bullfrogs 50 years later was likely due to the bullfrog presence on under-surveyed private lands, and temporal disparity between native amphibian and introduced bullfrog survey seasons (S. Ashpole pers. comm.). Lack of landowner awareness surrounding native and introduced amphibians is also thought to have contributed to bullfrogs not having been detected until 50 years later; the landowners who purchased the bullfrog-colonized properties were aware of bullfrog presence but thought bullfrogs were a native species (S. Ashpole pers. comm.).

The South Okanagan is an arid region home to a unique species assemblage within Canada. One half of the native amphibian species present are federally threatened, endangered, or of special concern (Species at Risk Act (SARA)). Along with over 84 % loss and degradation of aquatic habitat (Lea 2008), major threats to native South Okanagan amphibians are terrestrial habitat degradation and loss, road mortality, aquatic pollutants largely due to agriculture, and introduced predatory fish (Ashpole 2015, Bishop et al. 2010, Crosby 2014, Lesbarrères et al. 2014). Existing threats to native amphibian populations, combined with the limited overall detected locations, isolated nature of the colonized ponds, and wide body of literature suggesting bullfrogs negatively impact native wildlife, prompted conservation managers to prioritize bullfrog removal in the South Okanagan.

An on-going bullfrog control program was initiated in 2004 in a collaborative effort by university researchers, provincial and federal governments, local conservation organizations, local First Nations, and private land and business owners. Multiple detection and removal methods combined with public outreach were employed on an annual basis. The goal of this study was to: 1) describe the methods, total effort, and results of the bullfrog management; and 2) highlight key management lessons learnt through bullfrog control in the South Okanagan. Although the bullfrog control program also involved extensive public education and outreach, and funding and in-kind resources pieced together from various organizations, this account focuses on the effort specific to physical bullfrog detection and removal.

Methods

Study region

The Canadian portion of the Okanagan is located in the Okanagan sub-basin of the Columbia River, in the Pacific Northwest, North America. The South Okanagan region lies in central BC, extending north from the Canada-US border to Summerland (Figure 3.2). The land is approximately equally privately owned, Crown, and Indian Reserve (South Okanagan Similkameen Conservation Program (SOSCP) 2012). The valley is historically composed of rugged terrain at high elevations, open antelope-sagebrush grassland at mid to low elevations, and large lakes connected by the Okanagan River, wetland, and riparian habitat along the valley floor (Demarchi 2011). The region is classified as cold semi-arid according to Koppen climate classification, with annual precipitation levels of 319 mm and 38 % of the year experiencing daily maximum temperatures above 20 $^{\circ}$C (ECCC 2016).

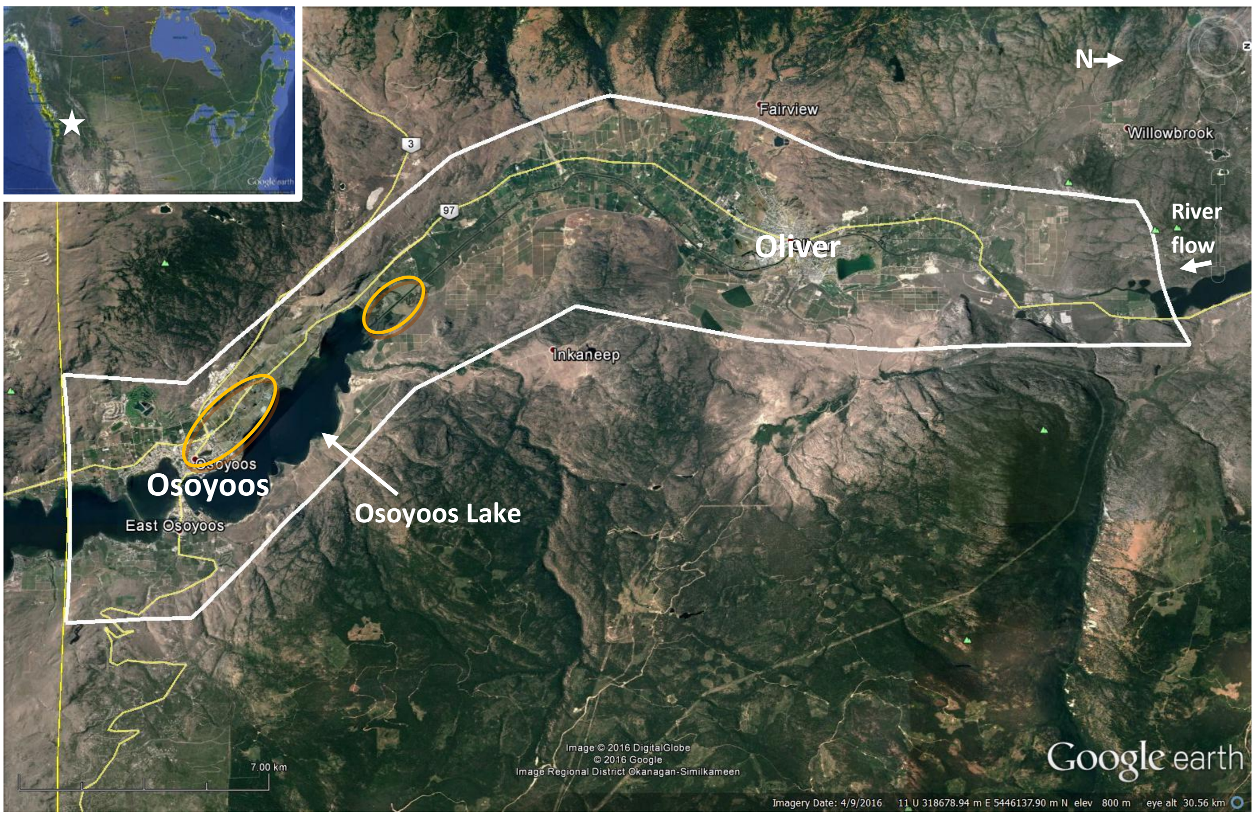


Figure 3.2. South Okanagan bullfrog management study area. Location of study area within Canada inset top left; "primary" 3 bullfrog-colonized ponds referred to in methods are circled in orange; yellow vertical line indicates Canada – USA border. Exact locations of bullfrog-colonized ponds remain confidential unless otherwise noted (modified from Google Earth 2016).

The study region is a complex matrix of agriculture interspersed with residential and industrial areas and patches of floodplain, riparian, and antelope/sagebrush grassland habitat. Three urban centers, Okanagan Falls, Oliver, and Osoyoos, support a total population of 19 000 people, and occur at the north, middle, and south border of the study area (Our Okanagan 2016). In addition to extensive wetland loss and modification, over 77 % of the natural grassland habitat has been converted for tree fruit, vineyard, and ground crop agriculture or urbanization since the early 1900s (Lea 2008). The study area between Vaseux Lake and Osoyoos Lake is connected by the channelized Okanagan River. The river channelization reduced river habitat by 93 % (Lea 2008) and resulted in multiple isolated, remnant oxbows and permanent water bodies staggered throughout the valley bottom, ranging in area from 0.05 ha to 10.6 ha. The Okanagan River also connects the study area from Vaseux Lake (278 ha) at the north end, to Osoyoos Lake (1480 ha) at the south border end of the study area.

Wetlands within the South Okanagan range widely in condition and surrounding matrix (Figure 3.3). Although few remain, the South Okanagan desert is characterized by ephemeral grassland depression wetlands, as small as 12 m^2, surrounded by shrub steppe grassland, or within remnant sections of the Okanagan River’s natural wet meadow floodplains or modified agricultural lands. Introduced predatory fish, such as bass (*Micropterus dolomieu and M. salmoides*) and carp (*Cyprinus sp.*), often breach the Okanagan River’s banks during high water, and are subsequently found in multiple ephemeral floodplain wetlands in spring and early summer. In addition to the larger lakes, smaller permanent water bodies present within the South Okanagan also range widely in area from < 0.1 to 50 ha and range in their presence of introduced predatory fish species. The complexity of the shoreline and emergent vegetation at the permanent wetlands also varies widely.

The primary bullfrog locations discussed below include Original Pond, Fish Pond, and South Okanagan Wildlife Management Area (SOWMA). Original Pond and Fish Pond occur in the Town of Osoyoos, and are both irrigation ponds within tree fruit orchards. Original Pond and Fish Pond are colonized by introduced invasive fish species, and both have limited riparian buffers less than 5 m wide dominated by introduced invasive vegetation such as phragmites (*Phragmites australis australis* and Siberian elm (*Ulmus pumila*). Both ponds occur in the low-point between rolling hills, though Fish Pond has steep shoreline of over 75 % slope in most areas around the perimeter. Original Pond’s shoreline is approximately 40 % slope in most areas around the shoreline, with a retaining wall along the east bank. SOWMA is located at the head of Osoyoos Lake, at the confluence of Okanagan River Channel and Osoyoos Lake. SOWMA is a semi-naturalized area with abundant native riparian buffer adjacent to grassy floodplain. SOWMA is composed of 4 oxbows in close proximity to each other and to flooded areas and small ponds.

Although the majority of water bodies surveyed for bullfrogs were relatively small floodplain wetlands, agricultural irrigation ponds, oxbows, or artificial ponds, the shorelines and bays along Osoyoos Lake were also surveyed.

Figure 3.3 South Okanagan bullfrog control program area habitat and wetland structure. Water bodies range widely in hydroperiod, size, depth, shoreline and aquatic vegetation, surrounding matrix, and introduced fish presence. All locations pictured occur near Osoyoos, BC; specific bullfrog locations remain confidential unless otherwise noted.

Detection and removal methods

Bullfrog detection and removal methods were initiated in 2004, following the first South Okanagan bullfrog detections in 2003. University, federal, provincial, and local non-profit conservation biologists and trained volunteers undertook landowner contact and wetland surveys at 125 known natural and human-made water bodies within the study region to determine the extent of bullfrog colonization (Ashpole 2015). Effort was then focused and increased in frequency at specific ponds where bullfrogs were detected. The primary surveyed ponds included Original Pond, Fish Pond, and SOWMA (Figure 3.2). Note SOWMA is composed of 4 oxbows and multiple flooded areas in close proximity and connectivity; these oxbows and flooded areas were regarded as one site for data analysis.

Multiple methods were employed to target each life stage from 2004 through 2012. Field work was co-lead by former University of Waterloo Graduate Student Sara Ashpole, BC Ministry of Environment's P. Govindarajulu, and Environment and Climate Change Canada's D. Cunnington through all years, while the author of this thesis undertook field work in 2010 –

2012. Night-time auditory surveys, night-time canoe searches, day time visual encounter searches (active searches), and modified floating and sinking Gee trapping were the main methods employed (Table 3.1). Isolation fencing (1.5 m buried and staked hardware cloth) and fence line box funnel traps were set at the 2 perceived heaviest bullfrog-colonized ponds and where shoreline conditions required little modification for installation, Original Pond and Fish Pond, in 2005 for 3 years. Additional methods utilized but not consistently employed across years included call-back surveys, fly-fishing, use of pellet guns, basking traps, electro-shocking, use of fishing spears, and seine netting. The seven aforementioned methods not consistently used over the years were excluded from analysis in this study.

Frequency of methods at each site depended on annual budget, and varied across years and by site from 2004 - 2012 (Tables 3.1 and 3.2). Generally, primary bullfrog locations were visited a minimum of 3 times per week, and up to daily for active searches and auditory surveys during the bullfrog egg laying period. Gee trapping was conducted from beginning of June through to at least end of July annually at Original Pond, and discontinued after the early years at the other two locations due to low return on effort. Non-bullfrog detected locations received active searches and auditory surveys minimum 4 times per year, with sites rotated among years due to the large number of survey sites in the study area. Non-bullfrog detected locations also received minimum one session of Gee trapping. Canoe searches were only used where bullfrogs were detected and the sites accessible by canoe, and along the shoreline of Osoyoos Lake. Seine netting was also only used in years tadpoles were detected by trapping or active searches, and once in 2012. When bullfrogs were detected, capture effort was adjusted accordingly at the detection site until all observed bullfrogs were removed.

An additional method, automated auditory recording, was implemented in 2011. Four Songmeter SM2+ (© Wildlife Acoustics) were rotated among 5 known bullfrog-colonized wetlands. Songmeters were set to record 10 hours per day, and were set from mid-May through mid-September in 2011 and each subsequent year.

Basic data regarding environmental conditions at time of capture or detection, wetland metrics, and morphometric data of individuals were collected for each survey session. Adults were occasionally checked for stomach contents and reproductive development. The life stage of individuals captured was also recorded. For the purpose of this discussion, life stages are labeled adult, juvenile, metamorph, tadpole, and egg mass. Juveniles included sub-adults, metamorphs included newly transformed tadpoles with tail still present, and all eggs within one egg mass were categorized as a count of 1. All individuals at Gosner (1960) stage 20 through 41 were labeled tadpoles.

Table 3.1 Main detection and removal methods used in the South Okanagan bullfrog management program. Methods Followed BC Provincial amphibian inventory protocol (MELP 1998) unless otherwise noted. Removal methods intensified at detection locations until all observed bullfrogs were captured.

Method	Target life stage	Effort unit	Description
Auditory surveys	Calling adult males	Detected/ not detected per observer hour	Observers visited water bodies visited between dawn and dusk on random occasions from May through minimum July. Observers recorded relative number of calling individuals based on standard scale of 0 – 3, representing a range of 0 individuals to a full chorus. Surveys were not conducted during rain and wind conditions over 3 on the Beaufort scale to minimize listening disruptions. Primary bullfrog ponds and adjacent water bodies surveyed minimum 8 times per year. Non-primary locations generally visited minimum 4 times per year. The length of survey varied from 5 to 20 minutes.
Active searches	Tadpoles, egg masses	Number bullfrogs per observer hour	Entire perimeter of shoreline searched for all life stages during daylight. Surveys not conducted during rain and wind conditions over 3 on the Beaufort scale to minimize visual disruptions. Primary bullfrog ponds and adjacent water bodies visited daily to minimum 3 times per week. Non-primary bullfrog locations generally visited minimum 8 times per year. Active searches by foot were also occasionally conducted at night using a flashlight.
Night-time canoe searches	Adults, juveniles	Number bullfrogs per observer hour	Conducted after dark at accessible bullfrog locations. Observers trolled the shoreline (approximately 4 km/hr) using a flashlight to detect eye-shine of adults and juveniles. Canoe searches varied in frequency depending on location and detection via other methods. Detected adults were manually caught using spear or dip-net, or shot using pellet gun*. Canoe searches conducted only at bullfrog-colonized ponds and Osoyoos Lake shoreline.
Gee trap	All	Number of bullfrogs detected per trap for 24- trap day equivalent	Partially submerged, baited 30 cm diameter Gee traps set along shoreline. Traps deployed from beginning of June through minimum end of July annually. Trap entrance modified to allow small adults entry. Trapping used in early years at all three primary locations, then reduced to only Original Pond following low return on effort at other locations. Traps were checked daily during peak activity periods, where capture rate was high, or where native species occurred, and were checked every 2 days otherwise.

*use of pellet gun conducted only by firearm certified individuals, including project lead and Conservation Officer.

Data analysis

Data were used with permission and originated from the BC Ministry of Environment, BC Ministry of Forests, Lands, and Natural Resource Operations, Environment and Climate Change Canada, and research conducted via the University of Guelph and University of Waterloo [4].

The majority of methods used in the South Okanagan bullfrog control program, with the exception of call-back surveys, were selected based on their use in bullfrog control methods in other regions, communications with researchers managing bullfrog control in other regions, and availability of resources (P. Govindarajulu pers. comm., Foster and Banks 2008, Kraus 2009, Louette et al. 2014, Marchant 2012, Nehring and Klingenstein 2008, Reinhardt et al. 2003, Spitzen-van der Sluijs and Zollinger 2010, Kraus 2009, Schwalbe and Rosen 1988, Adams and Pearl 2007, US Fish and Wildlife 2002, Orchard 2011). Detection and removals were targeted towards all life stages, and were largely opportunistic rather than being designed for experimental comparison purposes, due to funding and resource limitations. All removals followed Canadian Council on Animal Care Guidelines (CCAC 2012) and were conducted under BC Provincial Wildlife Act permit. Despite resource limitations, when detected, bullfrog removal efforts were intensified until all observed bullfrogs were removed. The nature of the data collection, in addition to the rotation of non-bullfrog colonized site surveys across years, presents limitations in post hoc data analysis and statistical comparisons among sites and methods. Descriptive statistics were selected for final data analysis, for the main methods used (Tables 3.2 and 3.3).

Data analysis was conducted in Microsoft Excel™. The dataset was separated into (Table 3.2):

1. "primary" locations, composed of Original Pond, Fish Pond, and SOWMA, where main survey methods were focused and/or the bulk of the bullfrogs were detected and removed; and
2. "other" locations, the remaining surveyed sites. Two of these sites contained bullfrogs, one of which only 2 dead carcasses were detected, and the other site was 12 m^2 in area and only a handful of bullfrogs detected. The remaining sites received less intense survey effort due to lack of bullfrog detections, and monitoring was rotated throughout the 2004 – 2012 period.

Catch per unit effort, accumulated catch, and total effort were calculated for the primary sites for each main method (Tables 3.2 and 3.3). Total effort and catch, and total individual catch by life stage and year were then also calculated for all the other sites combined (Table 3.2). Effort for auditory surveys, active searches, and canoe searches are expressed as the number of bullfrogs detected per hour by observer. Set trap methods, including Gee trapping and basking trapping,

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[4] University of Waterloo, Ontario; lead researcher Dr. Sara Ashpole
University of Guelph, Ontario; lead researcher Dr. Sara Ashpole
BC Ministry of Environment; lead researchers Dr. Purnima Govindarajulu and Laura Friis (retired)
BC Ministry of Forests, Lands, and Natural Resource Operations, lead researcher Orville Dyer
Environment and Climate Change Canada, Canadian Wildlife Service; lead researcher David Cunnington

are expressed in number of bullfrogs trapped per day by trap. Each "trap day" represents 24 hours of a trap being set.

Table 3.2 Data analysis conducted on bullfrog detection and removal data for 2004 – 2012 South Okanagan bullfrog management program.

Locations	Method	Metric recorded	Analysis
Primary (Original Pond, Fish Pond, SOWMA)	Gee trapping Active searches Canoe searches	Number of individuals	1. CPUE vs. accumulated catch (Krebs 1999) 2. CPUE and accumulated catch vs. year for each main method 3. Total time of effort by method
Primary	Auditory surveys	Chorus intensity (scale of 0 – 3; relative abundance)	1.Total detections and effort
Original Pond, SOWMA, Osoyoos Lake	Auditory recording	Chorus intensity (scale of 0 – 3; relative abundance)	1.Total detections and effort
All other locations (primary sites excluded)	Gee trapping Active searches Canoe searches	Number of individuals	1. Total amount of effort by method
All other locations	Auditory surveys	Chorus intensity (scale of 0 – 3; relative abundance)	1.Total detections and effort
All locations (primary and other)	All search effort and detections and removals	Number of individuals	1. Total number of detections and removals by life stage and year

Table 3.3 Data available for main bullfrog detection and removal methods, Gee trap, active search, auditory and canoe searches, from 2004 – 2012 bullfrog management in the South Okanagan. Available data represented by X.

		Original Pond	Fish Pond	*SOWMA
2004	Gee trap	X	X	
	Active search	X	X	
	Auditory survey	X	X	
	Canoe search			
	Other			
2005	Gee trap			
	Active search		X	
	Auditory survey	X	X	
	Canoe search			
	Other			
2006	Gee trap	X	X	
	Active search	X	X	
	Auditory survey	X	X	
	Canoe search	X		
	Other			
2007	Gee trap	X	X	X
	Active search	X	X	X
	Auditory survey	X	X	X
	Canoe search	X		
	Other			
2008	Gee trap	X	X	
	Active search	X	X	
	Auditory survey	X	X	X
	Canoe search			
	Other			
2009	Gee trap	X	X	
	Active search	X	X	
	Auditory survey	X	X	X
	Canoe search	X		X
	Other			
2010	Gee trap	X		
	Active search	X	X	
	Auditory survey	X	X	X
	Canoe search	X		X
	Other			
2011	Gee trap	X		
	Active search	X	X	
	Auditory survey	X	X	X
	Canoe search	X		X
	Other	X		X
2012	Gee trap	X		
	Active search	X	X	
	Auditory survey	X	X	X
	Canoe search	X		X
	Other	X		X

*Surveys were not conducted and bullfrogs not detected at SOWMA until 2007 (grey shading).

Results

Total bullfrog detection and removal effort and captures

A total of 11 102 introduced individual bullfrogs and egg masses were detected and removed at 7 of the 125 surveyed sites in the South Okanagan between 2004 and 2012 (Table 3.4). The Original (source) Pond contained the majority of occurrences, with 11 035 of the total 11 102 individuals. Except for SOWMA, the other sites where bullfrogs were detected, occurred within 2 km of the Original Pond, and accounted for 9 of the total number of individuals detected and removed (Table 3.4).

Table 3.4 Individuals captured by life stage at all sites surveyed (2004 to 2012).

Site	Life stage					
	Egg mass	Tadpole	Metamorph	Juvenile	Adult	Total individuals
Original Pond	20	10576	39	109	291	11035
Fish Pond	0	1	0	0	53	54
SOWMA	0	0	0	1	3	4
Other	0	0	0	4	*5	9
Total	20	10576	39	114	352	11102

*One of the "other" sites contained 2 dead adult carcasses and zero detections of additional living or dead individuals or egg masses.

Approximately 640 and 850 total search hours were expended for auditory and active searches respectively, and 24 670 total trap day equivalents conducted at all of the survey sites (Table 3.5). An additional 2 940 hours were spent on automated auditory recording, 65 hours on seine netting and night-time active searches by foot (Table 3.5). Ninety trap day equivalents were spent on basking trapping (Table 3.5).

Table 3.5 Total amount of effort applied for bullfrog detection and removal in the South Okanagan from 2004 – 2012.

Site	Method						
	Gee trap (24 hr trap day equivalents)	Active Search (search hours)	Auditory (search hours)	Canoe (search hours)	Auditory Recording	*Other (search hours)	Basking trap (trap days)
Original Pond	17360	210	80	95	980	65	90
Fish Pond	4860	190	25	0	0	0	0
SOWMA	25	10	170	145	980	0	0
All other sites	2425	440	365	70	980	0	0
Total effort	24670	850	640	310	2940	65	90
Overall CPUE	0.1 individuals/ day	0.6 individuals/ hour	0.1 detected/ not detected	0.2 individuals/ hour	0.0 individuals/ hour	115.4 individuals/ hour	10 individuals/ day

* includes active searches by foot at night, seining, and automated auditory recording and analysis. CPUE listed only for the other methods resulting in capture or detection

Individuals were primarily detected and removed in 2004, 2006, and 2008 (Figure 3.4). Zero detections occurred in 2011 and 2012 using any method including 2 940 hours of automated auditory recording.

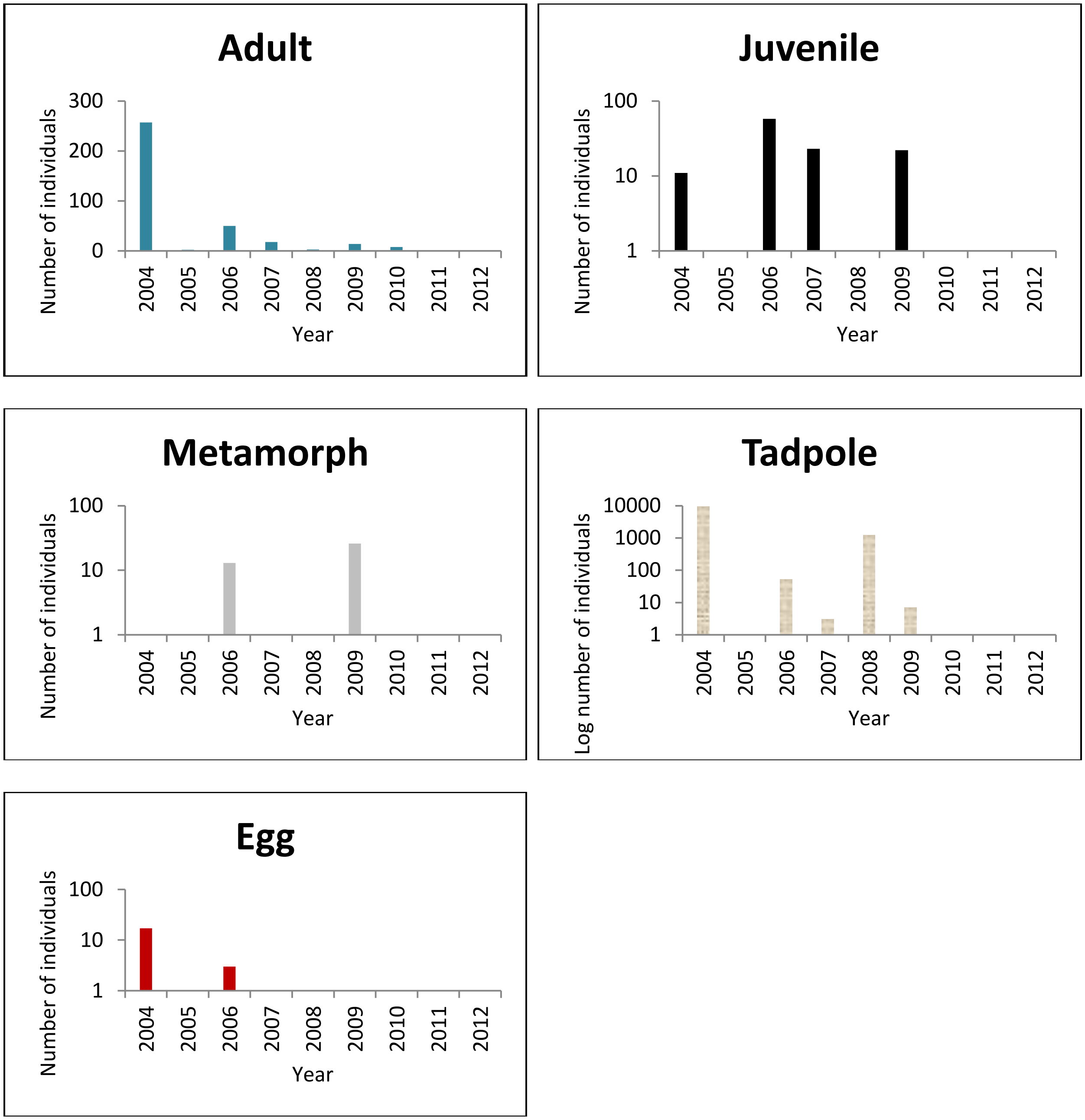


Figure 3.4 Total bullfrog individuals and egg masses detected and/or removed across sites by year.

Catch per unit effort and accumulated catch at primary bullfrog colonized sites

A number of methods were excluded from this catch per unit effort (CPUE) analysis due to their restricted use or small return on effort. Call-back surveys and basking traps yielded very little to no return, electro-shocking failed due to conductivity issues. Pellet guns, fishing spears, and fly-fishing were effective only with highly skilled individuals and when visibility conditions were high. Seine netting use yielded high return only when tadpoles were present in high abundance and environmental conditions were ideal (warm, clear, low to no wind).

Methods included in the main CPUE analysis were active searches, canoe searches, and Gee trapping. The CPUE varied largely between sites and within years. The CPUE ranged from 0 to 16 ± 55 individuals per trap day for Gee trapping, 0 to 41 ± 46 individuals per search hour for active searches, and 0 to 28 individuals per hour for canoe searches (Table 3.6 and Figures 3.5 and 3.6). For visual purposes, the variability surrounding CPUE is excluded from the figures and listed in Table 3.6.

Table 3.6 Variance in the mean annual capture per unit effort for the main methods at primary bullfrog locations (1 Standard Deviation reported with sample size in brackets). Years with no data collected are indicated by a dash. Sample size represents the number of sampling sessions used to calculate CPUE.

		Mean annual CPUE ± 1 SD (n)		
	Location	Gee trap (individuals per 24-hour trap day)	Active search (individuals per hour)	Canoe searches (individuals per hour)
2004	Original Pond	7 ± 22 (13)	25 ± 23 (18)	-
	Fish Pond	0 (8)	13 ± 15 (5)	-
	SOWMA	-	-	-
2005	Original Pond	-	-	-
	Fish Pond	-	0 (2)	-
	SOWMA	-	-	-
2006	Original Pond	2 ± 7 (17)	41 ± 46 (14)	28 (1)
	Fish Pond	0 (8)	10 ± 15 (9)	-
	SOWMA	-	-	-
2007	Original Pond	16 ± 55 (37)	1 ± 3 (16)	2 ± 0.5 (2)
	Fish Pond	0.1 ± 0.6 (27)	1 ± 2 (13)	-
	SOWMA	0 (5)	0 (5)	-
2008	Original Pond	0 (12)	0.1 ± 0.5 (32)	-
	Fish Pond	0 (5)	0 (33)	-
	SOWMA	-	-	-
2009	Original Pond	0.01 ± 0.02 (64)	1 ± 3 (65)	1 ± 1 (5)
	Fish Pond	0 (29)	0 (58)	-
	SOWMA	-	-	0.1 ± 0.1 (5)
2010	Original Pond	0 (11)	0 (62)	0.2 ± 0.1 (6)
	Fish Pond	-	0 (51)	-
	SOWMA	-	-	0.01 ± 0.05 (13)
2011	Original Pond	0 (1)	0 (33)	0 (5)
	Fish Pond	-	0 (33)	-
	SOWMA	-	0 (1)	0 (6)
2012	Original Pond	0 (9)	0 (44)	0 (3)
	Fish Pond	-	0 (16)	-
	SOWMA	-	-	0 (8)

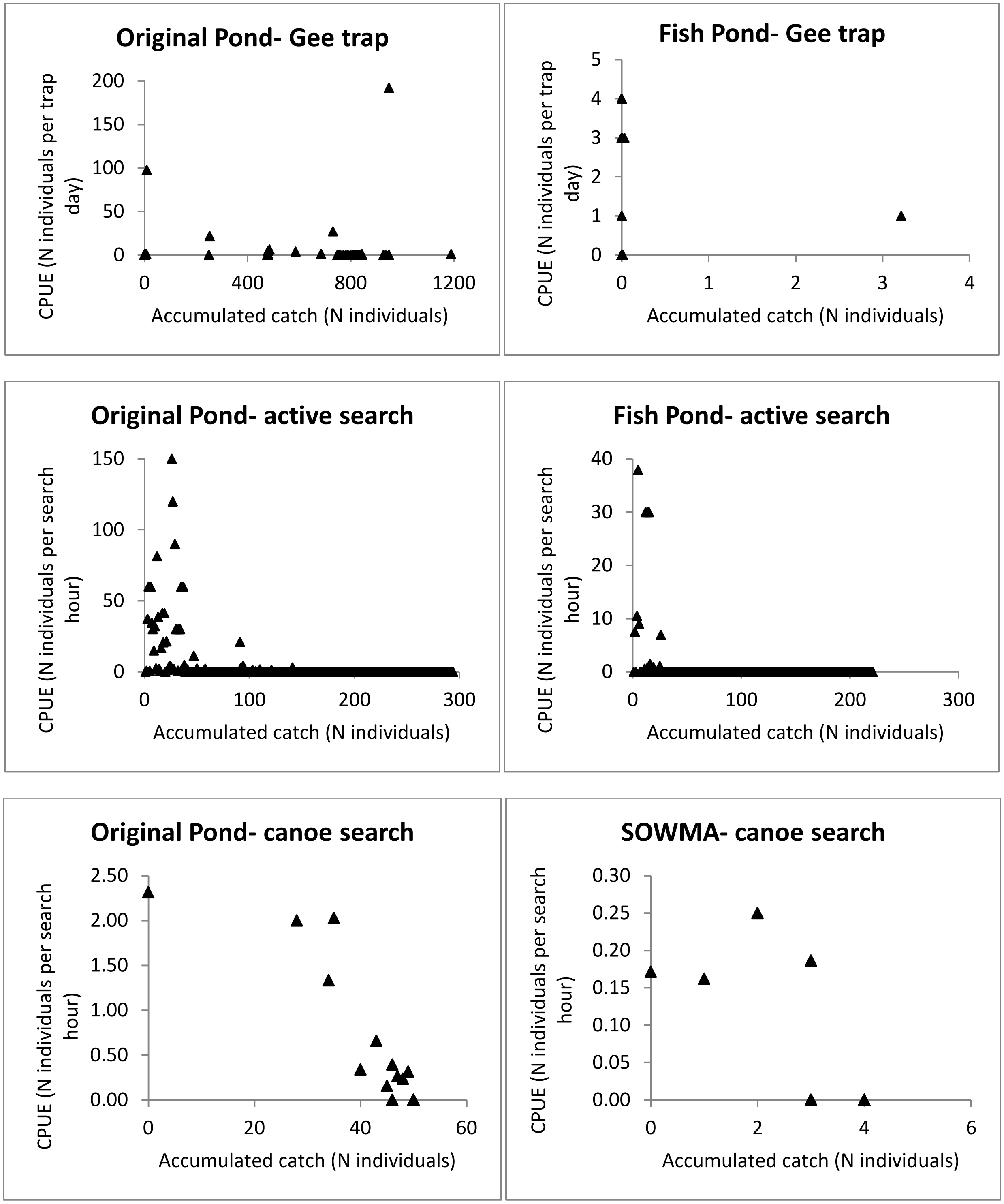
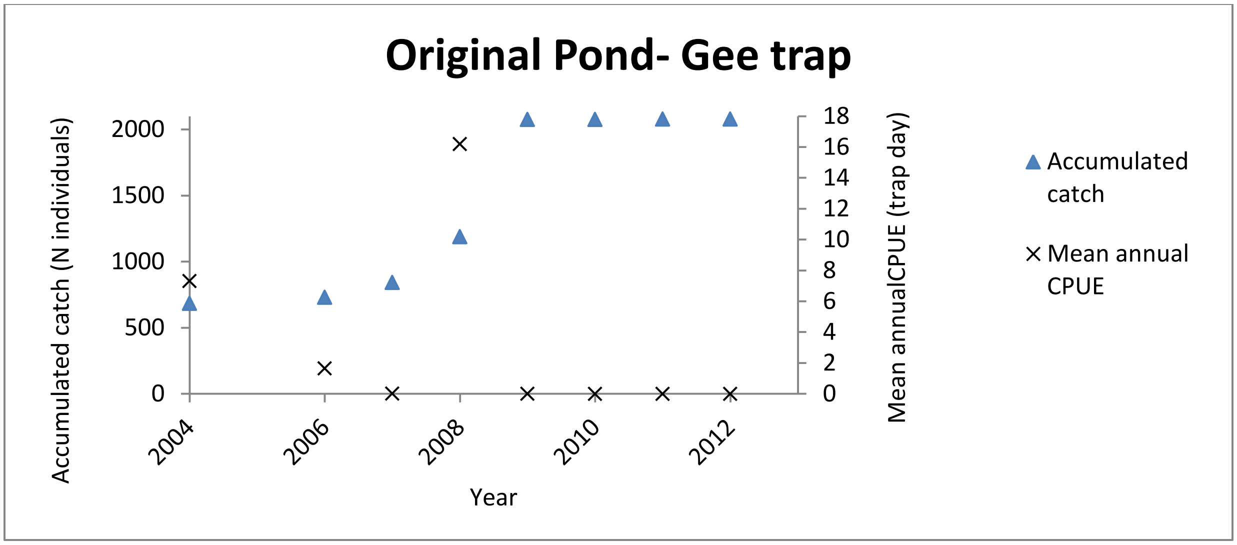


Figure 3.5 Accumulated catch vs. catch per unit effort for Gee trapping, active searches, and canoe searches for primary bullfrog sites. Note SOWMA excluded for Gee trapping and active searches, and Fish Pond excluded from canoe searches due to limited survey years and/or zero total detections.



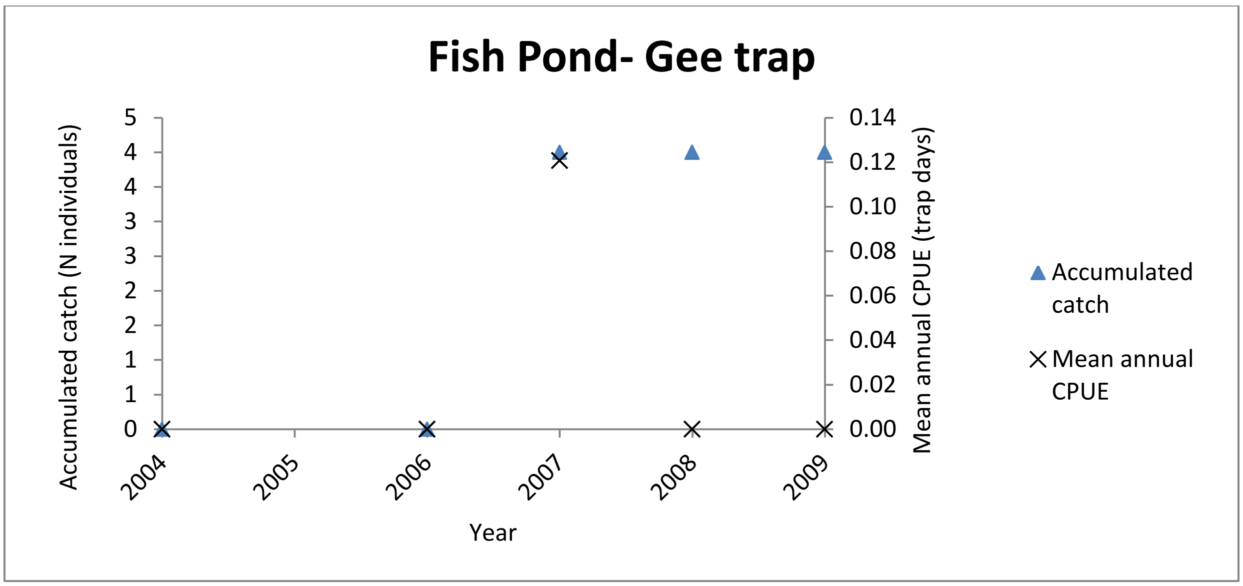
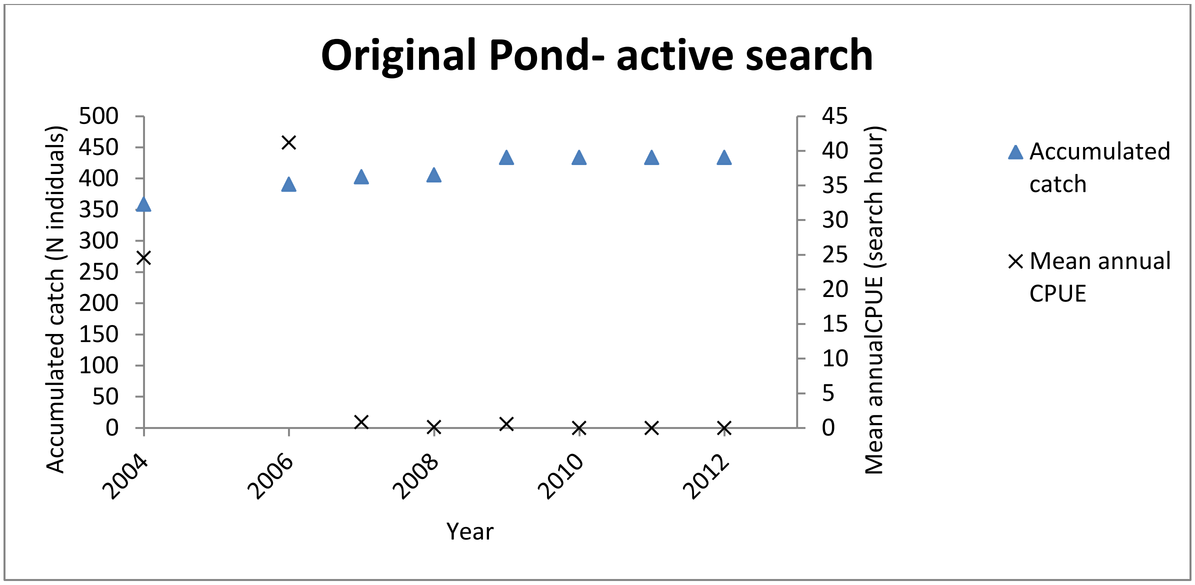


Figure 3.6 Catch per unit effort and accumulated catch by year for Original Pond and Fish Pond Gee trapping for bullfrogs. SOWMA site excluded from figure due to 0 captures and only 1 year of trapping. Variance omitted from figure for visual purposes, refer to Table 3.6 for details.



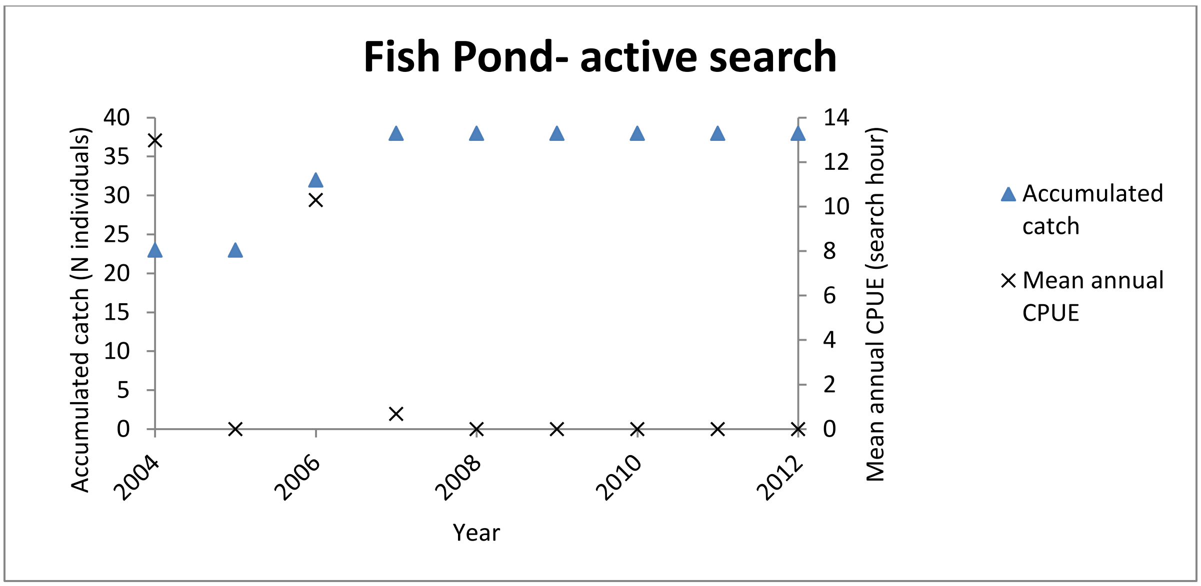


Figure 3.7 Catch per unit effort and accumulated catch by year for Original Pond and Fish Pond active searches. SOWMA site excluded from figure due to 0 captures and only 1 year of active search in 2007. Variance omitted from figure for visual purposes, refer to Table 3.6 for details.

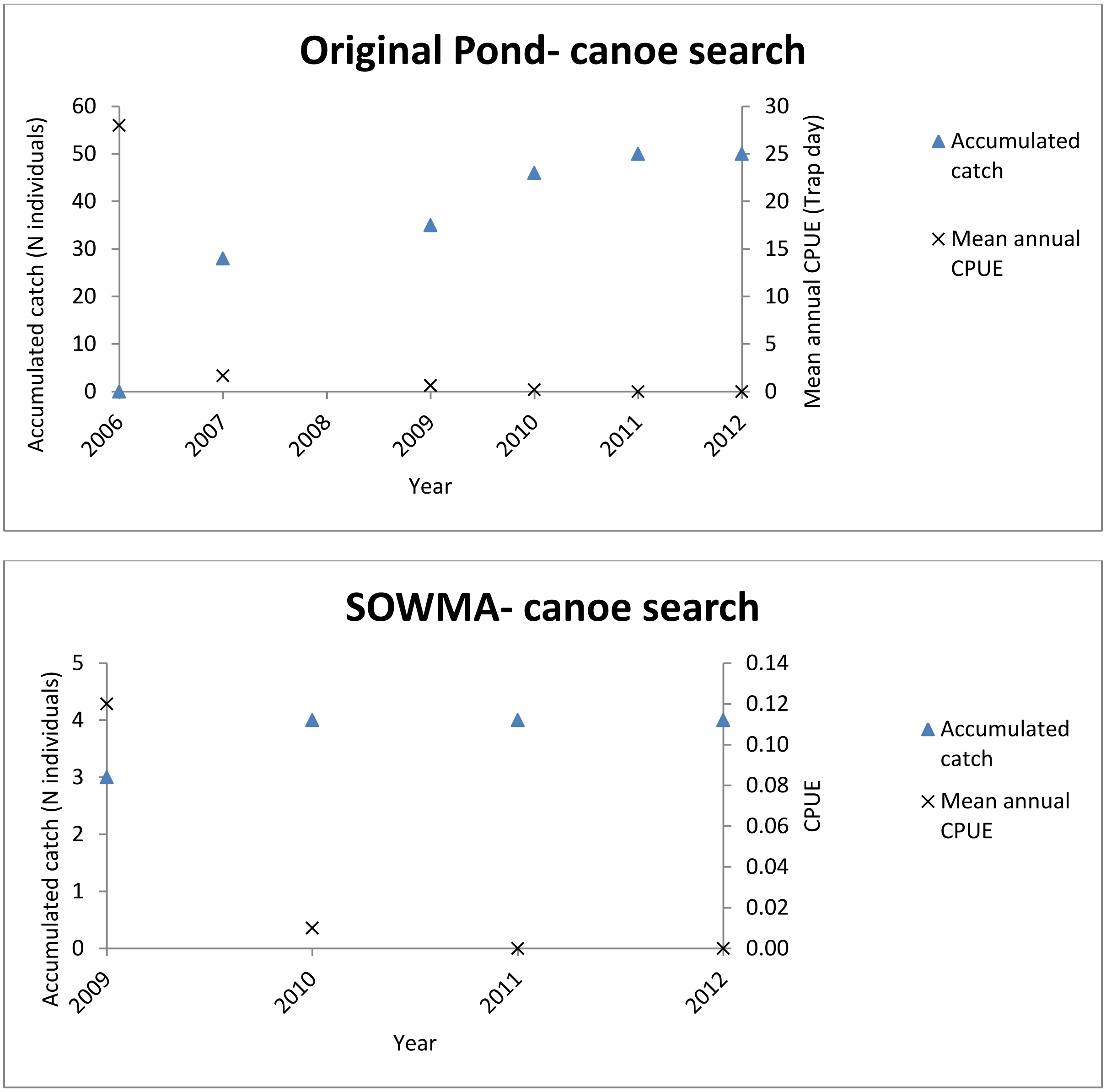


Figure 3.8 CPUE and accumulated catch by year for Original Pond and SOWMA canoe searches. Fish Pond site excluded from figure due to 0 captures and only 1 year of active search in 2007. Variance omitted from figure for visual purposes, refer to Table 3.6 for details.

Discussion

The goals of this study were to report total bullfrog detection and removal, describe the detection and removal effort involved, and discuss key lessons learned for bullfrog control in the South Okanagan from 2004 to 2012. Bullfrogs were observed at seven of the 125 total sites surveyed between 2004 and 2012. Multiple detection and removal methods were employed, though the main methods used and discussed below included day time active larval searches, night-time canoe searches, auditory surveys, automated auditory recording and Gee trapping. A massive amount of observer effort was conducted across the survey years: 24 670 24-hour Gee trap day equivalents; 850 active larval search person hours, 640 auditory survey person hours, 310 night-time canoe search person hours, and 2 940 automated auditory hours recorded. A high level of variation existed among detection rates for each method; however, overall bullfrog detections reduced to 0 in 2011 and 2012 suggest population suppression efforts are being successful. This variation in detection rates suggests monitoring should continue to ensure populations are suppressed. The length of continued monitoring is debatable, as information on successful eradication effort is largely unavailable, and management programs in other regions cite bullfrog reductions as “short-lived” (see Spitzen-van der Sluijs and Zollinger 2010). The following three sections expand on the recommendations for future monitoring, and the total effort, detections and removals, and management lessons resulting from the bullfrog management program in the South Okanagan.

Total bullfrog detections and removals

Bullfrogs were detected in 7 sites in over the initial 9 years of the South Okanagan bullfrog management program. Within the study, the number and stage of individuals varied across sites and years, but overall detections and removals decreased to zero by 2011 and population suppression remains (S. Ashpole pers. comm.).

Total bullfrog detections and removals declined across years with the exception of a sharp increase in 2006 and 2008. The reason for the peak in 2006 is unknown however, as the data available for 2005 are limited. The lowered abundance of detections and removals in 2005 may be due to: the removal of the majority of individuals in 2004; increased overall observer experience and detection skill; or may be an artifact of the data set. The 2008 peak occurred within a single pond, the Original (source) Pond. Monitoring effort was relatively consistent in 2007 – 2008, and the majority of detected adults present were removed previous to 2008. The sharp increase in tadpole and juvenile detections in 2008 – 2009 was likely due to undetected egg masses removed in 2007. The resulting eggs and juveniles in subsequent years may also have experienced predatory release and less resource competition from the lowered abundance of larger adults. Maintaining detection and removal pressure in these lowered abundance phases is critical to successful bullfrog population suppression.

Bullfrog populations are density-dependent, with survival to metamorphosis increased under low population density (Adams and Pearl 2007, Doubledee et al. 2003, Govindarajulu et al. 2005, Rosen and Schwalbe 1995). Successful bullfrog population suppression involves removal of all life stages, but with a focus on early metamorphosing tadpoles and juveniles (Adams and Pearl 2007, Doubledee et al. 2003, Govindarajulu et al. 2005, Kraus 2009). The current program attempted to address the above principle by eliminating egg masses and conducting seining and Gee trapping where tadpoles were detected to reduce metamorphic success.

Statistical population abundances were not estimated in the current study because of the large variance around capture rates, and the variance around the manner in which methods were implemented across years and sites. However, survey effort intensity remained high in 2011 and 2012, when zero detections occurred. Automated auditory recording devices also recorded for potential calling males throughout 2011 and 2012, with zero detections. The habitat conditions at the Original (source) Pond, particularly sparse shoreline vegetation, boost confidence that the decreased observed captures over time are relative to the decreases from initial abundance, at least at Original Pond. While some individuals may remain undetected at such low densities using standardized methods (Tanadini and Schmidt 2011), I can infer that the population is reduced from the original density at the Original and Fish Ponds. In contrast, the SOWMA sites are highly complex in habitat structure and therefore confidence in actual reductions is lower. The SOWMA location likely contains undetected individuals with potential to disperse to surrounding wetlands. Maintaining monitoring and removal pressure on remaining individuals is critical in keeping the remaining population at a low enough density for natural processes and stochastic events to extirpate the potential remaining population.

Five of the ponds were concentrated in a 2 km radius core, with the most heavily colonized breeding pond being the original introduction location (Original Pond). The four other colonized sites in the 2 km radius core occurred within 300 m from each other. Reproduction was detected at 2 of the primary ponds within the core, Original and Fish Ponds. Juveniles and adults were the only detected life stages at the remaining three ponds within the 2 km core radius. The adults and juveniles at the remaining three ponds were likely dispersed individuals from the Original and Fish Ponds. The two breeding ponds were irrigation ponds surrounded by tree fruit agriculture, colonized by introduced fish species, and heavily degraded. The remaining 3 ponds in the core varied widely in hydroperiod, shoreline vegetation structure and complexity, introduced fish presence, water body size and depth. The surrounding matrix connecting the remaining 3 colonized ponds were variations of urban and irrigated agriculture (ex. tree fruit and ground crops).

Adults and juveniles were also detected in two oxbows which occurred 5 km from the core area. The oxbows were adjacent to the Okanagan River Channel within a restored grazing and ground crop agricultural-use area. Both oxbows were heavily vegetated along the shoreline with native riparian tree and shrub habitat and introduced fish. Although the oxbows occurred 5 km away from the core area, the landscape between the core and oxbows included a 500 m urban/agricultural path to the lake, which eventually connects to the oxbows.

Bullfrog presence among the 4 wetlands in the core was consistent with natural, average dispersal of juveniles and adult bullfrogs (Corse and Metter 1980, Ingram and Raney 1943, Willis et al. 1956). Bullfrog presence in the furthest 2 colonized wetlands may be due to additional human-facilitated dispersal, but is also possibly due to natural dispersal along the lakeshore which connects the 2 furthest wetlands from the core area. However, the lack of detected breeding in 5 of the 7 colonized wetlands, and the large distance between the two main colonized areas despite bullfrogs known to have been introduced over 50 years ago suggests limiting factors in bullfrog dispersal and establishment in the South Okanagan. Introduced species often exhibit a lag period between introduction and establishment, potentially while the species adapts to the new environment (Sakai et al 2001). Little is known regarding bullfrog invasion ecology and lag periods; however, bullfrogs have colonized similar ecosystems and water bodies in the US to large degrees (Balfour and Morey 1999, Cunningham et al. 2007, Gahl et al. 2009). Bullfrogs are also highly fecund (Govindarajulu et al. 2004) and have established populations with as few as an estimated 6 individuals in other regions (Ficetola et al. 2008(a)). Introduced bullfrog populations also retain high genetic diversity relative to native populations, which aids in population persistence (Funk et al. 2011). The South Okanagan bullfrog populations may have still been in a lag phase, though three other factors are hypothesized to be limiting population growth and establishment:

1. The combination of predatory fish species, fish density, and wetland shoreline structure (P. Govindarajulu pers. comm.): although bullfrog colonization is often facilitated by introduced predatory fish (Adams et al. 2003, Boone and Semlitsch 2003), the bullfrog-colonized wetlands in the Okanagan are limited in escape opportunities for bullfrogs from the fish, the majority of which are carp (*Cyprinus carpio*) and bass (*Micropterus spp.*). The shoreline of the wetlands are structured such that fish have access to the majority of the shoreline up to the bank, allowing for full access to larvae and eggs. The predation rate on larvae may be enough to suppress potential reproduction effort of the bullfrogs. Introduced predatory fish species present may also be less discriminate against the palatability of bullfrogs, a factor offering survival advantage for bullfrogs with other fish species (Kruse and Francis 1977, Szuroczki and Richardson 2011). If applicable pending additional bullfrog detection in the ponds, diet analysis of co-occurring fish is recommended.

2. Lack of population establishment may also be related to water quality or chemistry, although the most heavily colonized ponds occur within locations most susceptible to water pollution.

3. The hot, dry South Okanagan climate may limit natural bullfrog dispersal, particularly in hot, dry years where fewer ephemeral ponds exist to act as dispersal stepping stones. The climate is generally very hot and dry during the bullfrog active season in the Okanagan, increasing chance of desiccation for the non-arid climate adapted species. If individuals cannot find moist movement corridors, they may be more susceptible to desiccation during their dispersal period. Although bullfrogs can move over dry, open fields (Willis et al. 1956, Youngquist and Boone 2012), dispersal in other hot, dry climates is thought to be limited by the climate (Luja and Rodriguez-Estrella 2011). Bullfrogs were detected in two main areas composed of ponds

situated in close proximity to each other, and with ponds either surrounded by riparian floodplain or irrigated tree fruit agriculture.

Regardless of whether dispersal may be limited in the South Okanagan by the habitat conditions, predatory fish dynamics, or arid climate, several water bodies throughout the valley present ideal habitat conditions as “stepping stones” to dispersal and bullfrog establishment, based on research conducted in similar regions (Balfour and Morey 1999, Cunningham et al. 2007, Gahl et al. 2009). I currently do not have confirmation about how bullfrogs dispersed to SOWMA, up to 5 km from Original Pond, or whether the individuals at SOWMA or elsewhere were progeny of Original Pond bullfrogs. Regardless of human facilitation or natural dispersal in the Okanagan, educating local residents about implications of bullfrog introductions is also critical to population suppression and prevention of re-introductions. The outreach and education component of the bullfrog management program is not discussed in this thesis, although continuing the outreach and education is also highly recommended as an important continued part of controlling this human-facilitated invasive species (Teillac-Deschamps et al. 2009). For additional detail on the outreach component of the South Okanagan bullfrog management program, see Lukey et al. (2012).

Bullfrog detection and removal effort

High variability surrounded bullfrog detection and removals across methods, sites, and within and among years. The variation in CPUE supports the premise that effort needs to be maintained for detection and removal in subsequent years as there are likely additional individuals at low enough densities to avoid detection by standard methods (Tanadini et al. 2011). Bullfrog management programs in other regions cite bullfrog population suppression as short-lived (see Spitzen-van der Sluijs and Zollinger 2010), and information on the length of bullfrog-free wetlands following eradication is unknown. A base monitoring time length recommended here is to follow The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recommendations for population trend assessments for threatened and endangered species (COSEWIC 2015). If perceived current abundance of bullfrogs in the Okanagan is in fact low, and the population treated as “threatened”, COSEWIC recommends a monitoring period of 10 years or 3 generations, whichever is longer (COSEWIC 2015). For the case of bullfrogs, 10 years is the recommended minimum monitoring period with zero detections at all previously known colonized sites. 2011 represents the first zero-detection year of monitoring; meaning detection and removal effort should be maintained until at least 2021.

The capture methods and total individuals caught, and the reduction in detection and removals indicates that the combination of methods selected was successful in reducing abundance at the colonized ponds. Each method presented advantages and disadvantages for the South Okanagan bullfrog management (Table 3.7).

Table 3.7 Advantages and disadvantages of main detection and removal methods used in the South Okanagan bullfrog management program.

Method	Advantage	Disadvantage
Gee trapping	Captured tadpoles, juveniles, and adults; captured a high number of individuals; can be conducted in any water body. Cages able to remain in situ for extended times.	Requires large amount of observer time; may put native species at mortality risk if bullfrogs and native individuals are confined to the same trap.
Active searches	Detects a diversity of life stages; minimal gear required; allows for behavioral observations and detections of native species.	Requires large amount of observer time; requires skill to manually capture detected individuals; limited by shoreline access and turbidity
Night-time canoe searches	Allows access to water bodies with dense shoreline vegetation (ex, SOWMA); can cover a large area in less time than active searches by foot. Water-side capture more effective than shoreline capture; allows for "eye-shine" detection over large shoreline area.	Only detects juveniles and adults; access to water bodies via canoe is limited at many locations; not effective in small water bodies; requires large amount of observer time
Auditory surveys	Relatively low observer effort required; cost-effective with respect to gear required	Requires training to minimize misidentification; may give false absence for low density or rare species; only detects calling males

The largest amount of observer effort was put into auditory surveys and active day time searches. Auditory surveys yielded lower life stage diversity detection. Auditory surveys also required slightly more effort per detection than active surveys, though significance of this difference is not known. Auditory surveys are commonly employed in amphibian monitoring protocols, and require less human and financial resources related to field gear and time for completion (BC Ministry of Environment, Lands, and Parks 1998, North American Amphibian Monitoring Program (USGS)). However, auditory surveys are less reliable for rare species (Crouch and Paton 2002, Dorcas et al. 2009), and bullfrogs are currently at low abundance in the South Okanagan with negative ecological consequences if they are not detected in a timely manner. Auditory surveys are also not a direct indicator of absence; when auditory surveys fail to detect calling, it simply means reproductive males were not detected, rather than lack of detection of all life stages.

Active searches are effective means of gathering information related to the occupancy and abundance of low abundance species and amphibians (Bower et al. 2014, MELP 1998), despite being more time consuming than other methods and relying more heavily on observer identification skill. Active searches combined with immediate removal also allow for capture of life stages which are optimal for bullfrog control, such as metamorphs. Early metamorphosing tadpoles may be one of the most efficient life stages to target for bullfrog population growth reduction, based on population studies of bullfrogs on Vancouver Island, BC (Govindarajulu et al. 2005). Active searches also provide information on species life history and behavior patterns of individuals. Information about behavior patterns is important when devising plans for removal of individuals. Comparison of auditory vs. active searches suggests that while valuable, for the purposes of continued bullfrog detections, a slight rebalancing of increased effort should be devoted to active searches at the primary bullfrog locations.

The final primary detection method, night-time canoe searches, received much lower observer effort than active searches and auditory surveys. Canoe searches required less observer effort per detection than auditory surveys, but more observer effort than active day-time searches. Canoe searches also captured less life stage diversity than active searches. However, canoe searches were most often employed when individuals were detected but not captured by other methods. Night-time canoe searches allowed for efficient capture of adults and juveniles sitting on shorelines. Canoe searches also allowed access into ponds with complex shoreline vegetation and substrate that was extremely muddy and unsafe to search by foot.

In addition to the primary active searches, auditory surveys, and canoe searches, and automated recording, which are targeted at detection, methods targeted towards removal were also employed. The primary removal method employed was Gee trapping. Gee traps were consistently set each year at both of the two breeding ponds, but were also deployed where bullfrog presence was confirmed at non-breeding ponds, and intermittently at the majority of other ponds to support a regional amphibian monitoring program (S. Ashpole et al., unpublished data). Gee trapping detected all life stages except eggs and inconsistently detected adults and juveniles across years. The most successful years of adult and juvenile trapping occurred during the lowest tadpole detection years. Despite inconsistencies, Gee trapping did support a large portion of total captures of all life stages, and should remain a removal method moving forward.

Seine netting was more effective than Gee trapping, though these results are likely skewed by the limited use of seine netting. Seine nets were employed in 2004, 2008 after the missed egg masses, and 2012. Seine netting was the most efficient method of tadpole removal, was moderately successful at adult removal, but was not an efficient means of juvenile removal. Seine netting was successful at detecting bullfrog tadpoles, but is limited by pond substrate conditions, depth, and size. Seine netting was also not a consistently used method in the South Okanagan due to hazardous conditions created by scrap metal and other garbage around the perimeter of Original Pond. The pond has since been cleared of the waste, making seine netting much safer and more practical should tadpoles be detected again.

The automated auditory recording Songmeters™ were initiated in 2011. The Songmeters™ did not detect any calling bullfrogs but did allow for an intense amount of surveying to be completed at sites where bullfrogs were known to exist in the past and likely still exist in very low abundance. The Songmeter™ analysis was challenging for sites closer to urban areas and roads because of the large amount of background noise interference. Airplane, tractor, and vehicle motors triggered false presence by the Songmeter™ software, as did other species with similar call frequency ranges, such as Canada Geese (*Branta canadensis*), Great Blue Heron (*Ardea Herodias*), and canines. The high rate of false negatives resulted in approximately 45 to 60 minutes of data quality control and analysis effort post-recording for every 4 hours of field recording. Despite the relatively large amount of effort required to analyze the Songmeter™ recordings post-field collection, the devices allowed for an intense amount of monitoring effort at the handful of ponds where bullfrogs were known to previously exist. If the observer analysis time to process recorded sessions can be reduced, the automated recordings may be advantageous where an intensive amount of listening time is required to detect the few remaining individuals (Dorcas et al. 2009). Attempts to reduce observer analysis time must be carefully weighed against the risk of producing false negatives though (Waddle et al. 2009).

Other areas have tried different methods: introducing predatory fish to suppress eggs and larvae (Louette et al. 2014), environmental DNA detection (Acevedo and Villanueva-Rivera 2006, Dejean et al. 2012, Ficetola et al. 2008(b)), double fyke netting (Louette et al. 2014), and pond drainage (Spitzen-van der Sluijs and Zollinger 2010). Native fish introduction is not recommended in the Okanagan, as the natural state of Okanagan wetlands is to be fishless and native fish are not adapted to anoxic water conditions in stagnant ponds. Further, many of the bullfrog-colonized ponds already contained introduced, predatory fish. Pond drainage was considered in the Okanagan but ruled out due to a high recharge rate and logistical issues of water displacement at such a high volume. Double fyke netting is recommended as a method to explore, particularly if tadpoles are detected again, due to the low cost, consistent capture rates, and relatively high efficacy (Louette et al. 2014). Environmental DNA detection, though limited in warmer water temperatures, can be 2 to 5 times more cost efficient than traditional auditory and visual surveys (Dejean et al. 2011, Dejean et al. 2012, Ficetola et al. 2008(b), Jerde et al. 2011)) and is also recommended for exploration in the South Okanagan. Collaboration and cost-sharing among agencies researching other aquatic species may exist. Developing a complimentary management system among resource management agencies is recommended in addition to collaboration. Identifying which organizations are most ideal for which management task, based on current organizational mandates and work plans, may also streamline resources.

Based on limited available published information, introduced bullfrog population eradication has been successful in a handful of other regions (Ficetola et al. 2007(a)), though long-term colonization-free results are unknown. Whether new methods are explored, or the primary methods revisited, monitoring must continue to be intense and repetitive within and among breeding seasons (Adams and Pearl 2007, Foster and Banks 2008, Kraus 2009). The bullfrog monitoring program needs to remain fluid and robust, using multiple survey types within years to optimize detection (Adams and Pearl 2007, Ficetola et al. 2007(a), Foster and Banks 2008, Kraus

2009, Simberloff 2005, Spitzen-van der Sluijs and Zollinger 2010). Decreased detection probability of low density populations (Tanadini et al. 2011) means monitoring effort must be maintained to prevent remaining individuals, or new human-facilitated introductions, from re-establishing. Unfortunately, resources are likely to be even more limited in subsequent years. Combining bullfrog monitoring with other species or habitat monitoring and with other organizations may help streamline resources. Citizen science may also be employed to reduce resources (Dickinson et al. 2012, Crall et al. 2010), provided a trusted group of volunteers and a strict "observe and report" standard is maintained to prevent negative impacts to native species due to misidentification (S. Ashpole pers. comm.).

Key messages and the future of bullfrog management in the South Okanagan

Multiple lessons were learned for bullfrog management in the South Okanagan. The first major lesson is e*ach site requires an adaptive and robust approach*. For example, SOWMA was not ideal for active searches based on the muddy substrate and thick shoreline vegetation, therefore canoe searches were conducted at a higher rate than active searches at this site.

Another lesson learned is that r*emoval efforts must be persistent*: maintaining effort despite setbacks is critical to introduced bullfrog population suppression, as demonstrated by the missed egg masses in 2007. However, maintaining monitoring effort is challenging when faced with a lack of secured funds and/or funding cuts. Stakeholder collaboration and combining target species monitoring programs may help alleviate limited resource pressure. Persistence is also critical in stakeholder communication. High turnover among park, land, and business managers also required persistence in education and outreach efforts. Persistence is also directly related to multi-year planning within agencies.

In addition to being persistent, r*emoval efforts must be ongoing*: though bullfrog abundances appear greatly reduced at the colonized locations, the high variability surrounding catch per unit effort throughout the survey period suggests detection and removal effort should continue. Ten years of zero detections is recommended (COSEWIC 2015) to allow at least 3 generations of potential metamorphs to reach maturity, existing adults to age, and natural and stochastic processes to extirpate remaining population. Following the 10 years of non-detection at the previously colonized ponds, monitoring can be included in the regular, less frequent region-wide amphibian monitoring regime. Bullfrog survival is density dependent and removing individuals from ponds leads to increased tadpole and early post-metamorphic survival, two very influential factors in bullfrog population viability (Adams and Pearl 2007, Doubledee et al. 2003, Govindarajulu et al. 2005, Rosen and Schwalbe 1995). Ponds not previously colonized should also remain under monitoring, though less frequently.

Future monitoring efforts should focus on additional active searches and fewer auditory surveys at the previously colonized ponds. Should additional bullfrog individuals be detected, exploring and revisiting double fyke netting, seine netting, and environmental DNA detection can also be initiated.

Maintaining consistency and accuracy in observer effort during long-term monitoring is challenging due to observer turnover, reliance on volunteers, and even when previously trained individuals do not develop adequate field experience. *Repetitive education is important for trained and non-trained volunteers:* in some cases, trained resource managers misidentified native species, such as the Columbia Spotted Frog (*Rana luteiventris*), for bullfrogs. Fortunately, the bullfrog program was well-known among stakeholders and biologists from the bullfrog control program were contacted regularly for identification confirmation. Regular training sessions were important in improving identification skills of previously trained professionals and new volunteers.

The future of bullfrog control in the South Okanagan presents challenges under low population abundance and low detectability, and reduced funding while population suppression is at a critical point in preventing re-establishment. Unfortunately, funding for the bullfrog management is likely to become even more limited than in the past. Potential funding sources often do not fund long-term monitoring, and bullfrogs are not known to cause significant harm to infrastructure or drinking water quality (Stitt et al. 2009), putting them at lower perceived rank than other regionally introduced species. Monitoring efforts will likely need to be pieced together over multiple collaborative projects. Potential collaboration ideas include: 1) Okanagan Nation Alliance: eDNA testing for various species; collaborating in the ONA/OIB lead carp fishery; Western Painted Turtle habitat enhancement projects; 2) Province of BC: Ministry of Environment and Ministry of Forests, Lands, and Natural Resource Operations: collaborating for eDNA detection of introduced zebra or quagga mussels in large water bodies and bays of the main lakes; Species At Risk Monitoring. Combining sampling sessions with other species may help to reduce overall costs in collection and analysis; and 3) Okanagan Similkameen Stewardship Program: developing a Habitat Steward citizen science protocol for landowner partners in areas with wetlands.

The above collaboration recommendations are in addition to the already extensive multi-agency collaborative management efforts in the region with most of the aforementioned agencies. These recommendations are also geared more towards methods use and developing a complimentary system, where tasks are assigned to agencies with matching capacities, rather than repeated effort being expended among various organizations (S. Ashpole pers. comm.). An additional element not discussed here are the financial resources utilized in bullfrog management in the South Okanagan. Conducting a financial analysis may also highlight areas where resources can be streamlined.

Continuing the monitoring effort and adapting collaborative relationships are key to maintaining this success. Habitat management may also facilitate the maintenance of bullfrog population suppression. The final recommendation here is to increase the wetland restoration efforts in the degraded ponds in the region, particularly the known bullfrog locations. Restoring hydrologic and structural conditions to favor native amphibians may help deter future bullfrog colonization, or at the very least, offer a slight advantage for native species by offering microhabitat refugia (Adams and Pearl 2007, Pearson and Mooney 2012). Current habitat restoration efforts are underway at one of the bullfrog ponds (S. Ashpole and A. Skinner, pers. comm.), offering an excellent research opportunity for native species re-colonization following bullfrog suppression.

The data analysis in this chapter suggests that the South Okanagan bullfrog management program has been a tremendous success to date, greatly reducing the presence of bullfrogs in the study area. Incorporating a slight adjustment of active search vs. auditory survey effort, developing complementary inter-agency management procedures, continuing monitoring 10 years post- zero detections, and improving the degraded bullfrog pond habitat will build on the incredible amount of collaborative effort and success already established in this program.

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